VOL. XIII JANUARY 1959 NO. 1

PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

IN THIS ISSUE: Pray—*Foliar Venation of* Bobea elatior • Bary—*Zooplankton in Identification of Surface Waters* • Wollaston and Womersley—*Structure and Reproduction of* Gulsonia annulata • Winkler—*A Mechanism of Color Variation in the West Coast Sea Hare* • Gosline—*A New Suborder of Hawaiian Fishes* • Reish—*A New Species of Polychaetous Annelid from Southern California* • Ramage —*Evapotranspiration in Hong Kong* • Stone—*Flora of Namonuito and the Hall Islands*

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Pattern and Ontogeny of the Foliar Venation of *Bobea elatior* (Rubiaceae)

THOMAS R. PRAY[1]

BEFORE A FULL UNDERSTANDING and appreciation of the various patterns of foliar venation can be attained there must be a greater knowledge of the ontogenetic processes which result in the diverse patterns of veins. The ontogenetic investigations to date suggest that there is a correlation between the shape and arrangement of the plate-meristem cells of the young leaf which produces the minor vein system and the pattern of the mature venation. In the case of the prevalent pattern in dicotyledons of polygonal areoles as exemplified by *Liriodendron* (Pray, 1954, 1955*a*), the plate meristem concerned is composed of small isodiametric cells whose planes of anticlinal division (with respect to the surface) are random; i.e., they are not oriented in any particular direction. The veins which comprise the mature minor venation are similarly disposed. In *Hosta* (Pray, 1955*b*, *c*), a monocotyledon, on the other hand, the intercostal venation (i.e., that between the primary veins), whose course is roughly at right angles to the course of the primaries, is derived from a plate of cells elongated at right angles to the primaries. Likewise, the study of Foster (1950, 1952) on the distinctive foliar venation of *Quiina* shows that the lineolate minor venation is derived from similarly oriented elongate cells in the plate meristem of the developing leaf.

The present study was initiated therefore to examine the ontogeny of another distinctive pattern of foliar venation as displayed by the leaf of *Bobea elatior*. The genus *Bobea* with five species is endemic to the Hawaiian Islands. An extensive survey (Pray, 1953: 172–264) of the tribe of the Rubiaceae in which it is placed, the Guettardeae (composed entirely of woody trees and shrubs), has revealed an astonishing variety of foliar venation patterns which exhibit varying degrees of expression of a lineolate disposition of the minor veins. The simpler patterns present in the Guettardeae appear to represent initial phases in the evolution of a markedly lineolate pattern of minor venation. *Bobea*, as a representative of those genera which display a lineolate pattern to a slight degree only, is of particular interest in broadening our understanding of variation in foliar venation and the ontogenetic processes which lead to such variation.

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MATERIALS AND METHODS

The writer is indebted to Dr. Sherwin Carlquist for providing the material which formed the basis for the present study. The material was collected on the Palolo–Mt. Olympus trail on the island of Oahu, Territory of Hawaii. Vegetative buds and leaves in various stages of development were preserved in FPA. A voucher specimen of the same material has been deposited in the Herbarium of the University of California, Berkeley (Carlquist H6, August 1953). Mature leaves and those in several stages of development were cleared with 2½ per cent NaOH to facilitate the study of the overall venation pattern. Sections were made at 7 and 8 μ, with a great predominance of paradermal sections which have been found to be especially important in ontogenetic studies of venation patterns. All sections were stained with tannic acid—ferric chloride—safranin with a weak solution of fast green used to further differentiate the safranin.

VENATION PATTERN

The leaf blade of *Bobea elatior* is broadly lanceolate and varies from 4.5 to 11 cm. in length and 2 to 4.5 cm. in width. As is true

of all members of the Guettardeae (indeed, of almost all Rubiaceae), the major venation of the leaf consists of a midrib with a pinnate series of secondary veins arranged in a camptodromous manner (Ettinghausen, 1861: xvi); that is, the extremities of the secondaries curve acropetally near the leaf margin. In addition to the secondaries there are other prominent but smaller veins which diverge from the midrib and extend toward the margins. These intermediate veins (Foster, 1950: 163) are, however, entirely enclosed within the panels or areas delimited by the secondary veins. Such areas will henceforth be referred to as intersecondary or intercostal panels. In actuality the distinction between some intermediate veins and strong tertiaries is arbitrary because the two do intergrade.

In the mature leaf, tertiary veins and veins of lesser categories are not readily distinguishable. Hence it is convenient to refer to the entire intercostal venation exclusive of the obvious intermediates as the minor venation. It is the pattern, histology, and ontogeny of the minor venation with which the present study is particularly concerned. In a cleared leaf (Fig. 1) the minor veins, except for occasional obvious tertiaries, are fairly uniform in size and relative prominence. The ultimate areoles (smallest units of mesophyll completely enclosed by veins) are delimited for the most part by veins of the fifth and sixth orders. However, for the above mentioned reason, vein categories within the system of the minor venation will not be considered in descriptions to follow.

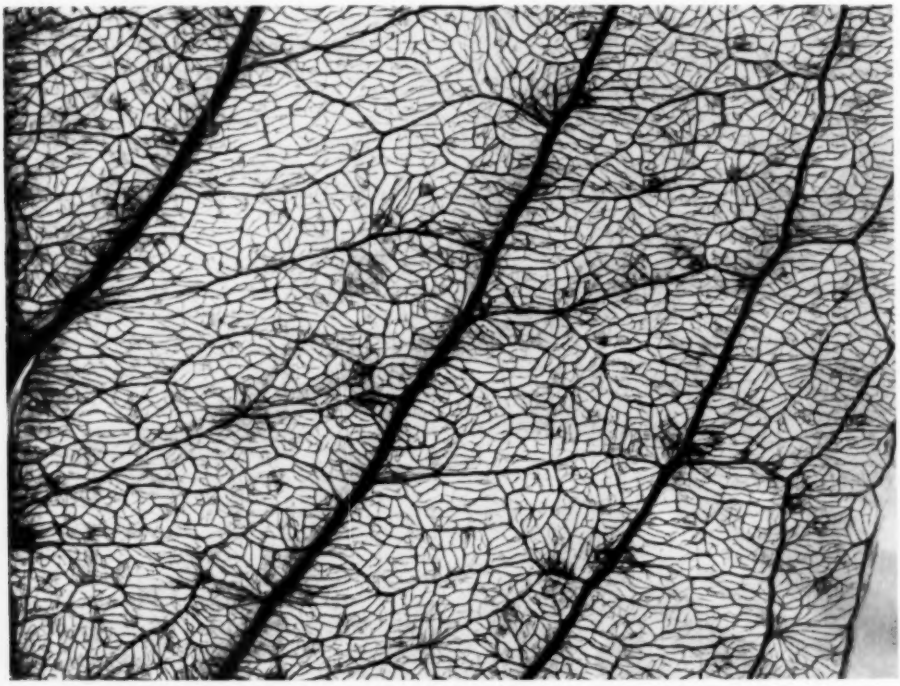
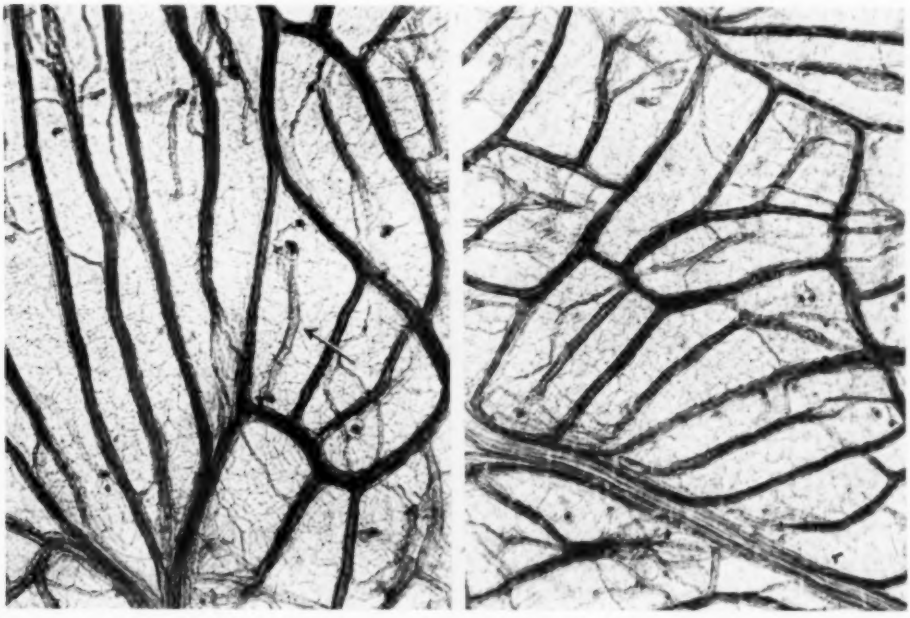
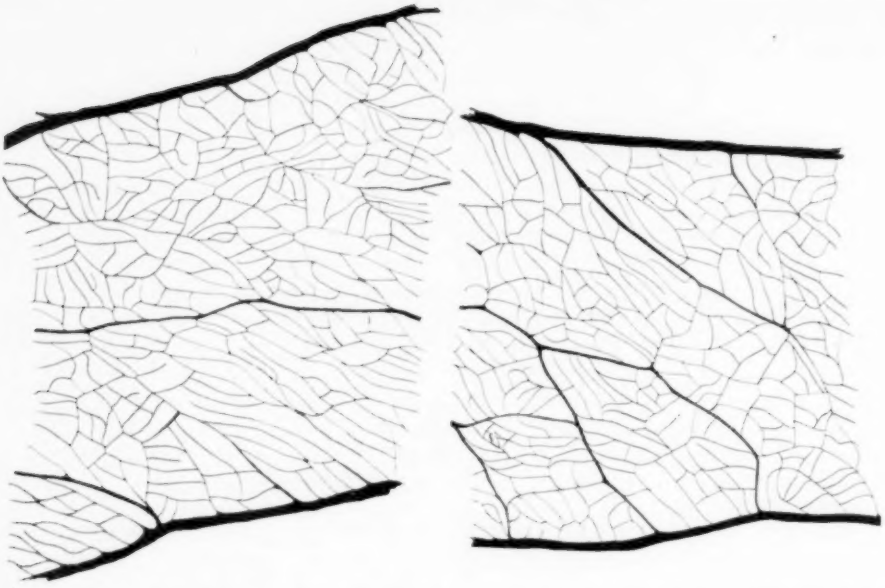


FIG. 1. Portion of a cleared lamina showing the general nature of the mature venation, × 7. Midrib at left; several secondary veins in part extend diagonally toward upper right.

The ultimate areoles of *Bobea* display a marked tendency to be rectangular and often distinctly elongated. While actual areole shape is extremely variable the tendency toward rectangularity is well enough expressed to give the minor venation a distinctive character which is readily distinguishable from the minor venation of such a leaf as that of *Liriodendron* and many other dicotyledons with their polygonal areoles. The tendency of the minor venation to be made up of elongated areoles is interpreted as a weak expression of the lineolate type of venation which becomes highly developed in some members of the tribe Guettardeae (Pray, 1953: 174–233). While the cleared leaf at low magnifications (as in Fig. 1) displays quite obviously the general character of the minor venation, the abundant sclerenchyma in the blade does obscure the details, particularly as regards the occurrence and nature of vein endings. There are fibers associated with every vein. In transverse section (Fig. 6) the fibers, which are located adaxial to the tracheary elements, are shown to comprise in fact the greater part of the vascular bundles. Strands of fibers and individual fiber cells extend from the vascular bundles into the mesophyll, in the region within the palisade layer, and between the palisade and hypodermal layers (Figs. 2, 3, 6). Careful study of cleared leaves at higher magnifications (Figs. 2, 3) shows that structures appearing to be vein endings are actually devoid of conductive tissues as such and consist of sclerenchyma only. Thus drawings of the true conductive system (Figs. 4, 5) show that most of the areoles lack vein endings. The latter are rather rare, in fact, in the present material. Apparently areoles without freely terminating vein endings are infrequent in the foliar venation patterns of dicotyledons in general (Esau, 1953: 424).



FIGS. 2 (*left*), 3. Small areas of the cleared lamina showing the nature of the ultimate areoles. × 65. Note fibers extending from the veins into the mesophyll. Arrow in Figure 2 indicates an idioblastic sclerenchymatous element.



FIGS. 4, 5. Drawings of portions of two intersecondary panels (secondary vein at top and bottom of each figure), × 10. Note scarcity of free-terminating vein endings.

LEAF HISTOLOGY

The general arrangement of tissues of the lamina of *Bobea* is distinctive enough to merit comment in this account. The epidermis is uniseriate on both leaf surfaces with the stomata limited to the lower. Beneath the upper epidermis there is a two-layered hypodermis (Fig. 6) of rather large, closely-packed cells apparently lacking chloroplasts. Ontogenetically, the hypodermis is derived from a single ground meristem layer. The latter is the adaxial subprotodermal layer which in many leaves produces the palisade layer of the mesophyll or its equivalent. The systematic significance, if any, of the hypodermis in the Rubiaceae is not known. It does occur in the only other species of *Bobea* (*B. timonioides*) available for study and in at least one species of *Timonius*, a closely related genus, but has not thus far been found in other genera of the tribe (Pray, unpublished). Solereder (1908: 445) and Metcalfe and Chalk (1950: 761) record the sporadic occurrence of this feature in several other genera of the family. The palisade layer, which is nearly medially situated in the leaf, is biseriate for the most part. The spongy layer is quite loosely arranged, with the individual cells of rather irregular form.

The smaller vascular bundles which constitute the minor venation extend from the lower limits of the hypodermis into the spongy mesophyll, with the conductive tissues located within the latter. As noted above, the greater part of the vascular bundle is sclerenchymatous, with individual fibers and fiber strands extending beyond the limits of the conductive tissues. There are rarely idioblastic sclerenchymatous elements in the areoles (Fig. 2, center). These often appear to be intermediate between typical fibers and elongate foliar sclereids, such as certain of the unbranched types described in *Trochodendron* (Foster, 1945: pl. IV).

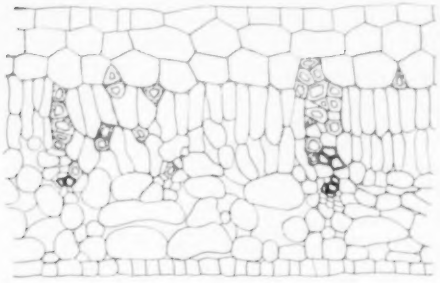


FIG. 6. Transverse section of mature lamina showing general leaf histology, × 200. Tracheary elements indicated with black walls; sclerenchyma with stippled walls.

ONTOGENY OF THE VENATION

Throughout blade ontogeny a basipetal pattern of maturation prevails, both in the initiation of secondary veins and in the differentiation of the minor venation between the secondaries. When the intersecondary panels are first delimited the cells of the plate meristem which will produce the minor venation are essentially isodiametric (Figs. 8, 17). The insertion of new cell walls anticlinal to the surface during this phase is apparently random. In a panel of such isodiametric cells, localized, oriented divisions in a continuous series of cells produce the first procambial strands (tertiaries) (Fig. 9) in a manner similar to that described for *Liriodendron* (Pray, 1955*a*: 21). Concurrent with the differentiation of the tertiary procambial strands the nature of the intervening ground meristem becomes noticeably altered with the establishment of a general tendency for the cells to become markedly longer than wide (Figs. 7, 10, 13). This condition is due largely to repeated cytokinesis of a given meristem cell in the same plane producing small packets of similarly elongated cells (Figs. 10–14). Similar divisions in two or possibly three contiguous cells can produce the same effect. The latter apparently happens infrequently because there is a decided tendency for the planes of cell division in adjacent cells to be completely unrelated and, in fact, they are rather frequently more or less perpendicular to one another. The tendency for small parallel groups of ground meristem cells to be formed, each independently oriented with respect to their neighbors, is characteristic of the ground meristem during the phases of leaf development concurrent with the formation of the minor venation as illustrated by examples in Figures 10–13. In a given section (Figs. 10–13) elongate cells are not evenly distributed. Sometimes small areas will display considerable regularity while others of the same leaf will have a rather sporadic expression of this tendency. It is from such parallel groups of cells that series of similarly oriented procambial strands are delimited (Fig. 16). Thus the essential nature of the minor venation of *Bobea* is determined by planes of cell division in the ground meristem immediately preceding procambial differentiation.

In the development of the minor venation (exclusive of obvious tertiaries) the delimitation of the procambium from the ground meristem appears to follow a rather orderly procedure when studied in paradermal section. A series of elongate cells derivable from subdivisions of a single cell or several adjacent cells is formed in this process. Most of these will subsequently redivide perpendicularly to the previously predominant plane of division, while one or sometimes several remain undivided. The elongate cells thus delimited are precursors of procambial strands. This series of steps can be illustrated by the following figures. In Figure 11 (top) there is a group of cells elongated perpendicularly to the course of the two procambial strands delimiting the areole. If, then, two or more of these cells remain undivided while the intervening ones further subdivide by a series of divisions at right angles to their long axes, the initials of procambial strands separated by a group of nearly isodiametric cells which are potentially ground tissue will be delimited. This apparently has occurred in Figures 12 (upper left) and 14 (upper right). This same

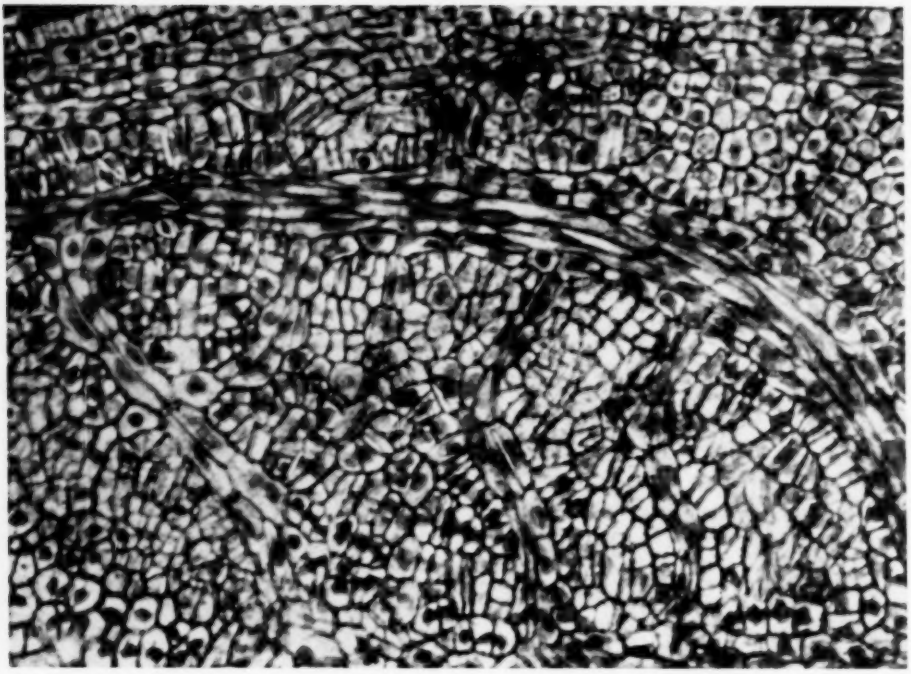


FIG. 7. Paradermal section of very young lamina showing about one half of an intersecondary panel with differentiating tertiaries, × 725. Leaf midrib at lower edge; leaf margin at top. Prominent procambial strand extending from right to left is a secondary vein.

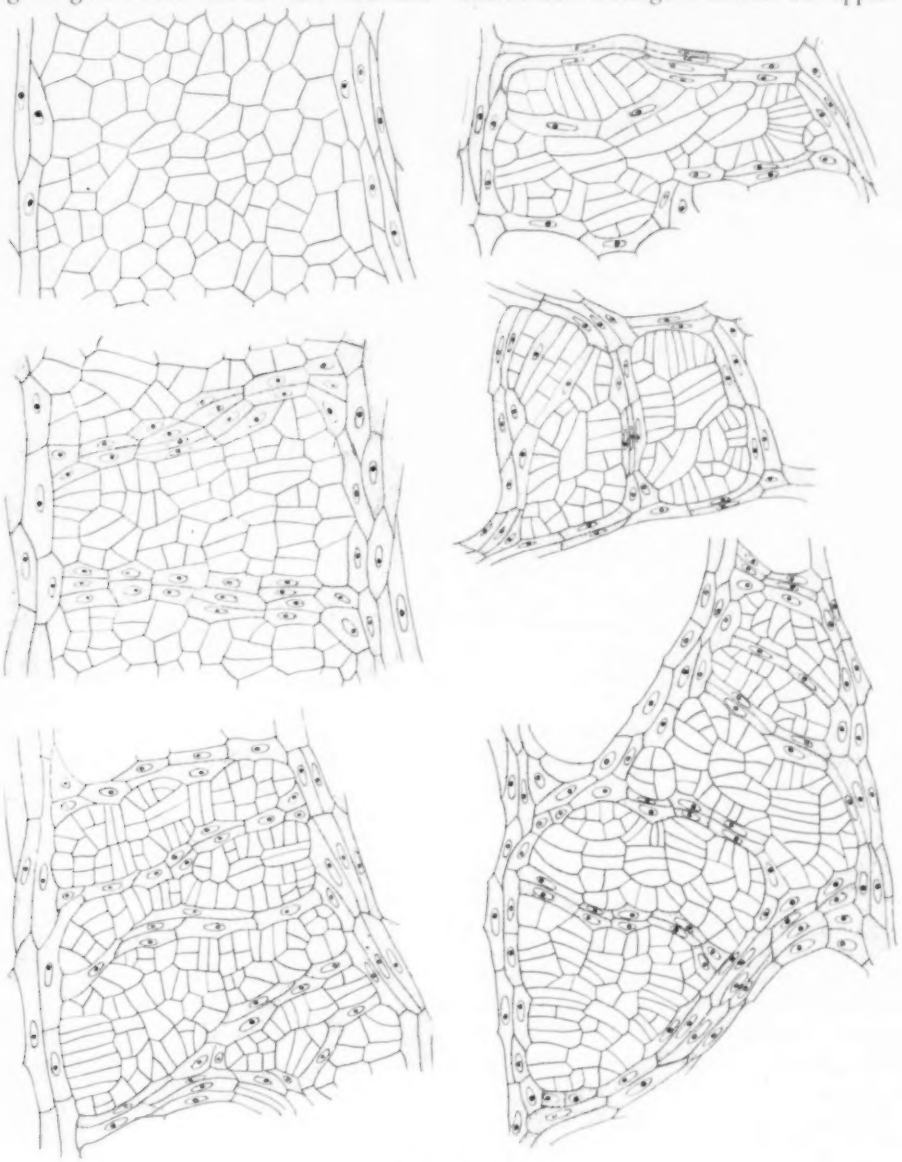
process has progressed farther in Figure 16. Thus areoles are produced which in the mature leaf often occur in more or less parallel series (see also Fig. 21).

During the differentiation of much of the minor venation, particularly below the quaternary category, there is a predominance of strands which are initially single celled (as seen in paradermal section). This is particularly true where a series of similar areoles have been delimited in a precise geometric manner as described above (Figs. 13–15). Most often, on the other hand, strands which apparently were initially more than one cell in length are curved (Fig. 16). Also included in this category are those forked strands (Fig. 15, upper half) which delimited areoles of various irregular perimeters.

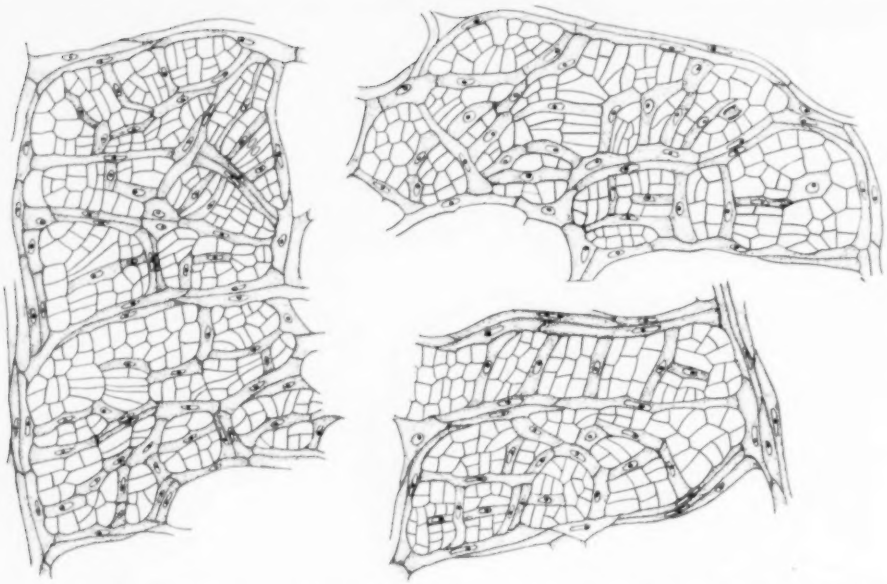
Much of the minor venation of *Bobea* shows less parallel orientation of veins than the preceding account suggests. This is directly attributable to the fact that much of the original

FIGS. 8–13. Portions of paradermal sections illustrating stages in the initiation and early ontogeny of the minor venation, × 700 (except Fig. 8, × 1000). Figure 8 (*upper left*): Intersecondary panel prior to appearance of any intersecondary procambium. Figure 9 (*middle left*): Similar panal with differentiated tertiary procambial strands. Note change in shape of ground meristem cells as compared with preceding figure. Figure 10 (*lower left*): Panel similar to Figure 9 in which subdivision of the ground meristem has proceeded further. Transverse procambial strands are tertiaries. Figures 11 (*upper right*) and 12 (*middle right*): Similar small areas illustrating the general nature of the ground meristem at the time quaternaries are being delimited. Figure 13 (*lower right*): Portion of intersecondary panel (midrib at left) with tertiary procambial strands. Another portion of the same panel is shown photographically by Figure 7.

ground meristem does not have the degree of precise parallel subdivision described in the foregoing ontogenetic series. However, the right-angled intersection of most veins and the general rectangular nature of the ultimate areoles is related to the tendency for veins and intervening panels of mesophyll to be derived from rectangular initials. The appar-



FIGURES 8–13

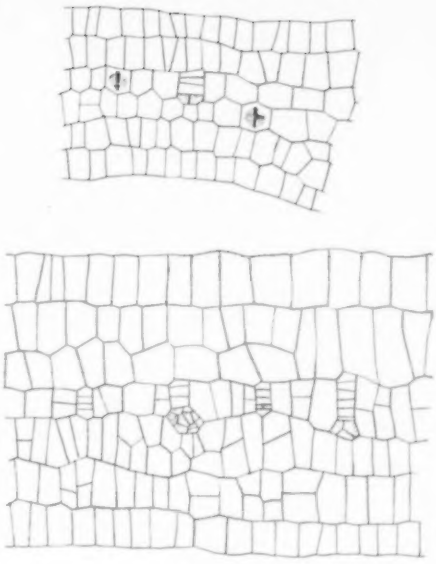


FIGS. 14–16. Portions of paradermal sections in which ultimate areoles are probably being delimited (or have been delimited). × 500. Figure 14 (*left*): Secondary vein at left margin; other large veins in these figures are tertiaries and quaternaries. (Fig. 15, *top right*; Fig. 16, *lower right*.)

ent random spatial relationship among various small groups of minor veins is a result of the apparent random planes of cytokinesis in each original ground meristem cell as compared with its neighbors.

A comparison of transverse sections in successive stages of leaf ontogeny (Figs. 17, 18) demonstrates that the sclerenchyma and vascular tissues of a vein have a common origin from an original procambial initial by a series of longitudinal divisions periclinal to the leaf surface. The lowermost cell or several cells then subdivide in various longitudinal planes to produce a strand of narrow procambial cells. During the earlier phases of differentiation these two components of the fibrovascular system of the leaf are not readily distinguishable in paradermal section. Therefore, it is only in the later phases of leaf development that we can distinguish clearly the future sclerenchyma from the actual conductive tissues. Figures 19 and 20 show the same area of a lamina at two levels; Figure 20 shows a section 12 μ closer to the upper surface than Figure 19. In Figure 19 there are shown a number of probable ultimate areoles delimited by obvious procambial strands, forming a pattern characteristic of the mature venation of the species. At this level in the relatively immature lamina (15 mm. long) the plate meristem has apparently been fully segregated into procambium and fundamental tissue with a reversion to a completely random insertion of anticlinal walls producing groups of more or less isodiametric cells (viz., Fig. 8). Apparently no more procambial strands are to be formed at this level. Just 12 μ above the latter section we find the pattern much more intricate and apparently still in the process of differentiation. The cells delimited from the ground tissue in Figure 20 are the initials of the sclerenchyma. Careful examination of the figures under discussion reveals that in addition to a series of

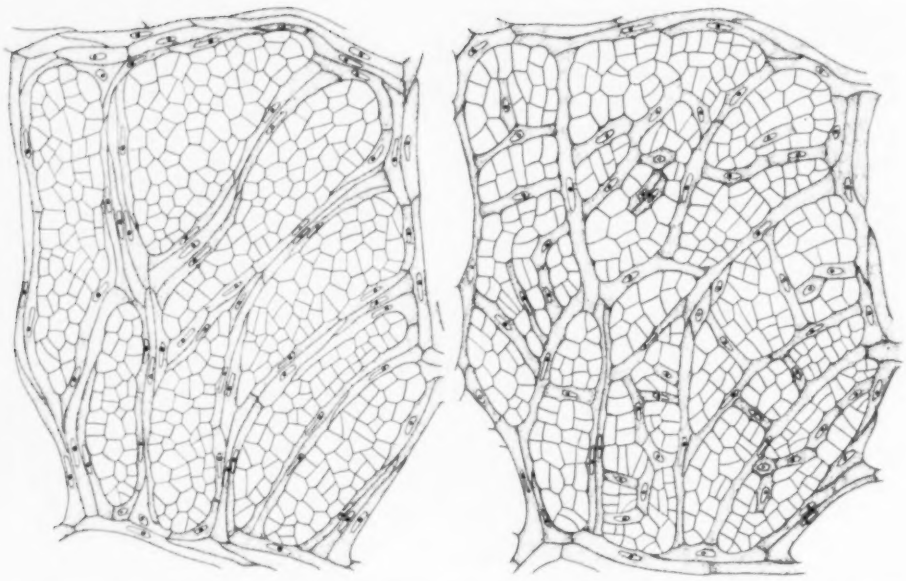
initials being present above each procambial strand there are also at the higher level numerous additional anastomoses. The latter mature into sclerenchyma. Also noteworthy in Figure 20 are the several initials which end freely in the ground tissue. These are the precursors of the abundant fibers which extend into the mesophyll in the mature lamina. Quite infrequently idioblastic cells (Fig. 20) are encountered which are presumably the initials of the occasional idioblastic fibers or fibro-sclereids which occur in the leaf of *Bobea*. Finally it may be noted that the ground tissue at the level of Figure 20 appears to retain a greater predominance of rectangular cells, suggesting that cell division is still active with the possibility of further differentiation of sclerenchyma continuing later than at the level of the clearly distinguishable procambium. The continued meristematic activity of this region is understandable in view of the late maturation of the palisade typical of dicotyledonous leaves in general.



FIGS. 17, 18. Transverse sections of laminae at two stages of development, × 500. Figure 17 (*above*): Original 6-layered condition (between secondary veins) with differentiation of a tertiary in the third layer from the adaxial surface. Figure 18 (*below*): Several stages in the development of minor veins and the occurrence of periclinal divisions in the various subprotodermal layers. Stippling indicates provascular initials as distinguished from those cells directly above which will become the sclerenchymatous portion of the bundles.

DISCUSSION

The older literature pertaining to the ontogenetic aspects of foliar venation and the modern histogenetic accounts have been reviewed and discussed by Foster (1952: 752–755) and Pray (1955*c*: 701–706). The present account of the leaf of *Bobea* appears to substantiate the ontogenetic pattern suggested in the latter paper. Namely, there is a definite correlation between the shape and arrangement of the plate meristem cells which gives rise to the vein system and the venation pattern of the mature leaf. In fact, a remarkable similarity will be found when the pattern of cell shapes in the ground meristem (Fig. 13) is compared carefully with the pattern of areoles in the mature leaf (Figs. 2, 3). The pattern of polygonal areoles constituting the minor venation of the leaf, as exemplified by *Liriodendron*, is of very widespread distribution in angiosperms. It is assumed as a working hypothesis that such a pattern is a basic type from which the distinctive venation types displayed by the Quiinaceae and certain members of the Rubiaceae have evolved by parallel trends toward a lineolate disposition culminating in a lineolate orientation of the entire intercostal venation. The venation of *Bobea* may be considered to be typologically intermediate between that of *Liriodendron* and *Quiina*. It is therefore interesting to note that the ontogeny of the foliar venation presented in this paper also may be regarded as intermediate between the two known extremes. In *Bobea* the first intercostal veins are delimited at a time when the insertion of anticlinal cell walls in the plate meristem which produces procambium for the minor venation is apparently random. The tertiaries and quaternaries thus delimited display a pattern in the



FIGS. 19, 20. Paradermal sections of the same area of a lamina at two levels after the ultimate areoles have been delimited, × 500. Figure 19 (*left*) represents a section 12 μ below that in Figure 20, showing a group of areoles enclosed by well-developed procambial strands. The panels of ground tissue will become mesophyll. Figure 20 (*right*): Same area 12 μ higher showing pattern of superimposed sclerenchyma, much more intricate, still actively differentiating apparently.

mature lamina which is not basically different from that of *Liriodendron*. In the intervening areas of the plate meristem concerned there is, then, a decided tendency for groups of elongate cells to be produced by series of similarly oriented cell divisions. From these groups are finally differentiated parallel-oriented minor veins delimiting areoles which are markedly elongate with a tendency to be rectangular rather than polygonal. In this respect, *Bobea* to some extent resembles *Quiina*, in which the entire intercostal venation is derived from a plate of embryonic cells in which the general orientation of elongate cells clearly foreshadows the mature, highly lineolate venation. It is therefore concluded that the ontogenetic sequence in the development of the lamina of *Bobea* represents a divergence in its later aspects toward that of *Quiina* which correlates with its difference in foliar venation pattern.

A critical evaluation of the above hypothesis must await the results from additional ontogenetic studies. Further investigations in the tribe Guettardeae would be highly rewarding, since in this apparently natural group there is such a wide variety of venation patterns. It is hoped that appropriate material of members of this group can be obtained to augment the present investigation. Similar studies should also be made of other representatives of the *Liriodendron* type of venation to test whether the postulated correlation here presented does indeed exist. In addition to intensive investigation of selected venation types there is also the need for more extensive surveys, such as have been initiated by the author in the Rubiaceae, to further our under-

FIG. 21. Illustrating the general nature in paradermal section of the ground meristem and procambial reticulum at a median phase of leaf development, × 600. Secondary at extreme upper left.

SUMMARY

standing of variation in foliar venation and the significance of such variation in systematics.

The foliar venation of *Bobea elatior* has been described. The distinctive feature of the venation pattern is a minor vein system composed of elongate, similarly oriented areoles, usually lacking vein endings. Thus the minor veins produce in some areas of the lamina a lineolate effect. An ontogenetic investigation of the lamina showed that the elongate areoles making up the minor venation are derived by a fairly precise differentiation process from a plate-meristem of markedly elongate cells, whose arrangement clearly foreshadows the vein pattern of the mature leaf. A comparison is made between the development of the venation of *Bobea* and that of other known types.

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Species of Zooplankton as a Means of Identifying Different Surface Waters and Demonstrating Their Movements and Mixing

B. M. Bary[1]

"In an area where several water bodies mix . . . the plankton animals alone can give the clue as to the water's origin unless the salinity differences are marked." Russell (1935) makes this statement during discussion of the indicator species *Sagitta elegans* Verril and *S. setosa* J. Müller from the English Channel and southern Irish Sea, and he has shown that when the two species occurred together, they were indicative of mixed waters. The remark suggests the possibility that more general use could be made of zooplankton organisms to indicate the origins of the waters in an area of mixing.

Russell's investigations concerned an area already comparatively well known faunistically and hydrologically, which is not true of the waters about New Zealand. A means has been needed whereby indicator species can be selected and utilized to demonstrate the sources, movements, and mixing of the waters for such little known areas. Two recent developments have assisted the realization of this. First, Miller (1950) used the temperature-salinity (T–S) diagram to show the origins and interrelationships of the several waters contributing to a mixture over an area of the continental shelf near Cape Cod. Second, Pickford (1946, 1952) has shown that the occurrences of the squid *Vampyroteuthis infernalis* Chun, when related (in the conventional T–S diagram) to the temperature and salinity at its points of capture, are confined in certain water masses. Similarly Haffner (1952) and David (1955) demonstrate environmental control over the distributions respectively, of several species of the bathypelagic fish *Chauliodus*, and of the chaetognath *Sagitta gazellae* Ritter-Zahony. An important corollary of this latter method is that representatives of the fauna of a water mass may be selected as indicators of the water through the relationships demonstrated to temperature and salinity.

The investigation by Miller concerned waters entering near-coastal areas; that of Pickford, and others, has been concerned with relating occurrences of species to particular oceanic water masses. By combining relevant procedures from the two techniques it would be reasonable to expect that the occurrences of zooplankton organisms could be viewed in relation to the waters entering, and in, a coastal area. Data from collections of plankton, temperatures, and salinities could then be evaluated in three general and related ways. From the combined diagrams it should be possible to identify a water body entering a particular locality, to select species which are representative of the fauna inhabiting that water, and to pursue the subsequent history of that water both from its own distribution and from the distributions of the selected species.

These several possibilities are investigated in the following account from data collected in oceanic and coastal waters, and their mixtures, about southern and eastern South Island, New Zealand. The collections are typical of those of many small scale surveys, but they were not intended for the present purpose and, therefore, are not ideal in certain respects. However, they do in fact demonstrate that the several possibilities may be realised.

The combined temperature–salinity and plankton (T–S–P) diagram is believed to con-

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tribute towards an objective determination of the indicator species in an area as comparatively little known as that about southern New Zealand. Further, the distribution of the species in the diagram can be used to confirm the distribution of the different waters. Salinity and temperature changes may take place over shorter, or longer distances, but may not be readily related to variation in the plankton occurrences. In the T–S–P diagram both physico-chemical changes in the environment, and the response to these of planktonic organisms, are demonstrable.

ACKNOWLEDGEMENTS

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MATERIALS AND METHODS

The collections of this study were made during surveying operations of H.M.N.Z.S. "Lachlan" during January, February, and March, 1951. Stations were occupied between Wellington and the Auckland and Campbell islands (Figs. 1, 2), and data are from surface samples. Temperatures and salinities have been obtained for all stations; in addition, temperatures were usually taken at regular intervals between stations. Salinities and temperatures of subtropical water have been included from a cruise between Wellington and Auckland via the west coast of North Island (small, open circles in Fig. 3 and see pp. 21–23).

The temperature and salinity data from the above sources have been used to construct the T–S diagram (Fig. 3). All stations are included. Those for which only physico-chemical data are available are differentiated from those at which plankton tows were made as well.

Surface plankton collections were made at 65 of the stations (see Table 4). Hauls were of three minutes' duration, and procedure and gear were carefully standardised (Bary, in press). Samples have been analysed quantitatively and the order of abundance of the selected species has been entered on Figures 5 to 10. The quantitative treatment is of value, but its importance is reduced in the present study since samples were taken at varying times in the 24-hour period (see p. 19).

A scale of smaller increments thanis usual in reporting on quantitative plankton analyses has been used in this study. They have been adopted because the short hauls frequently resulted in only small numbers of organisms being captured (see Table 4). It was necessary that occurrences of species in these small catches be adequately distinguished in order to detect whether there were reactions of species to changed environmental conditions and if these might be of ecological value.

Stations can be grouped conveniently into several series, as they were occupied during individual cruises (Series 4, 5, 6, and 7) or, failing this, in a particular area (Series 1, 2, and 3). In general, a series is spread over a

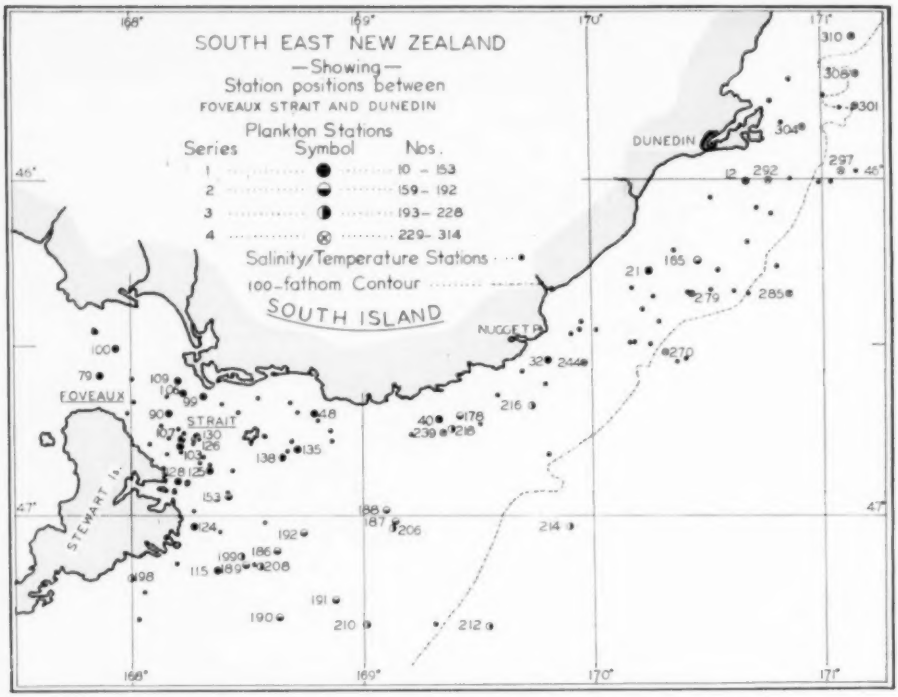


FIG. 1. Temperature/salinity and plankton stations in and about Foveaux Strait, southern New Zealand. Only plankton stations are numbered.

few days except for Series 1, in which stations accumulated irregularly over a period of 18 days; however, the stations are mostly from Foveaux Strait (Fig. 1). Information about the series is summarised in Table 1. In Figures 1, 2, and 3, each series of stations is symbolised separately; in subsequent figures this has not been practicable and for these it is necessary to locate stations in Figures 1, 2, or 3.

The method develops in two stages. In the first, each species is plotted, showing the order of its abundance, in the intercept of the salinity and temperature for all stations at which it was taken. In effect, species occurrences are superimposed on the T–S diagram to produce the temperature–salinity–plankton (T–S–P) diagrams (Figs. 5–10; note that the scale of Figs. 3 and 10 differs from that of Figs. 5–9). The correlations of specie and water properties thus demonstrated, together with previous distributional records of the species, have enabled species to be selected which occur consistently within those ranges of properties typifying certain water bodies. These species are indicator species, and 25 have been selected. They form into four separate groups (Tables 3, 4), each of which is considered to represent the planktonic population normally associated with a particular range of environmental conditions. Figure 10 summarises the interrelationships of these four groups. In the second stage, the distribution of each group in the T–S–P diagrams is correlated with the geographic distributions of both the group and properties of the waters. In this way, those similarities and differences of the planktonic content between sta-

TABLE 1
THE STATION SERIES, THEIR LOCATION, AND PERIODS OF OPERATION

SERIES NO.	STATIONS NOS.	DATES	NO. OF DAYS	GENERAL LOCALITY OF STATIONS
1	10–153	5–6 to 24.I.51	18	Foveaux Strait and southeastern New Zealand
2	159–192	29.I to 1.II.51	3	
3	193–228	5 to 13.II.51	8	
4	229–314	8 to 9.III.51	1	
5	1–6	3 to 4.I.51	1	Between Wellington and Dunedin
6	320–343	21 to 22.III.51	1	
7	795, 826, 921	13 to 17.XI.51	4	Between southern New Zealand and Auckland-Campbell islands

tions or groups of stations in the T–S–P diagrams, are considered geographically in relation to the distribution of the water properties which result from the movements of water bodies relative to one another.

SOME GENERAL CONSIDERATIONS

Either the method proposed in this study, or that adopted by Pickford, may be used to select those species which are indicative of oceanic water masses. An alternative use of the present method is to select those species which are indicative of the environmental conditions in a particular, restricted, and little-known area. However, in a wider survey, one or more of these same species may be found in such a variety of conditions as to render them valueless as indicator species. Most of the indicator species in the present study are regarded as useful throughout the area considered, but it might well be necessary to select other indicators for a locality with hydrologic conditions dissimilar to those found in the eastern and southern waters of New Zealand.

The occurrences of two species in the present survey illustrate these remarks and, at the same time, demonstrate the feasibility of using species other than those which previous information would suggest as suitable indicators for the waters in the area. *Thysanoessa gregaria* Sars is a tropical–subtropical–cool-temperate euphausiid which occasionally occurs in subantarctic waters (Sheard, 1953; Boden, 1954). However, it occurred as a breeding population in this survey, sometimes in high numbers, between the southern Auckland and Campbell islands and the subtropical convergence, i.e., in waters believed to be of subantarctic origin. *Cyllopus magellanicus* (Amphipoda) and *Eucalanus acus* (Copepoda) have similar distributions and are typical subantarctic species (Barnard, 1930; Farran, 1929). *Paracalanus parvus* is a widespread copepod (Wilson, 1932; Vervoort, 1949). Brady (1915) recorded it as "fairly common" to 64° 34.5′S. (in 127° 08′ E. long.) and at Auckland Island. In the present study, *P. parvus* occurred consistently, in large or very large numbers, in water believed to have originated in the subantarctic and become warmed in its progress northward. It was associated with *Euphausia lucens*, which is recognised as inhabiting warmer northern subantarctic waters (John, 1936), and with *Sagitta serratodentata* var. *tasmanica*, a "cold-tolerant" species (Thomson, 1947, and see p. 31). A few other species, e.g., among the Amphipoda, could be discussed similarly. These are species for which previous distributional records are at variance with the usage in this survey. However, it can be demon-

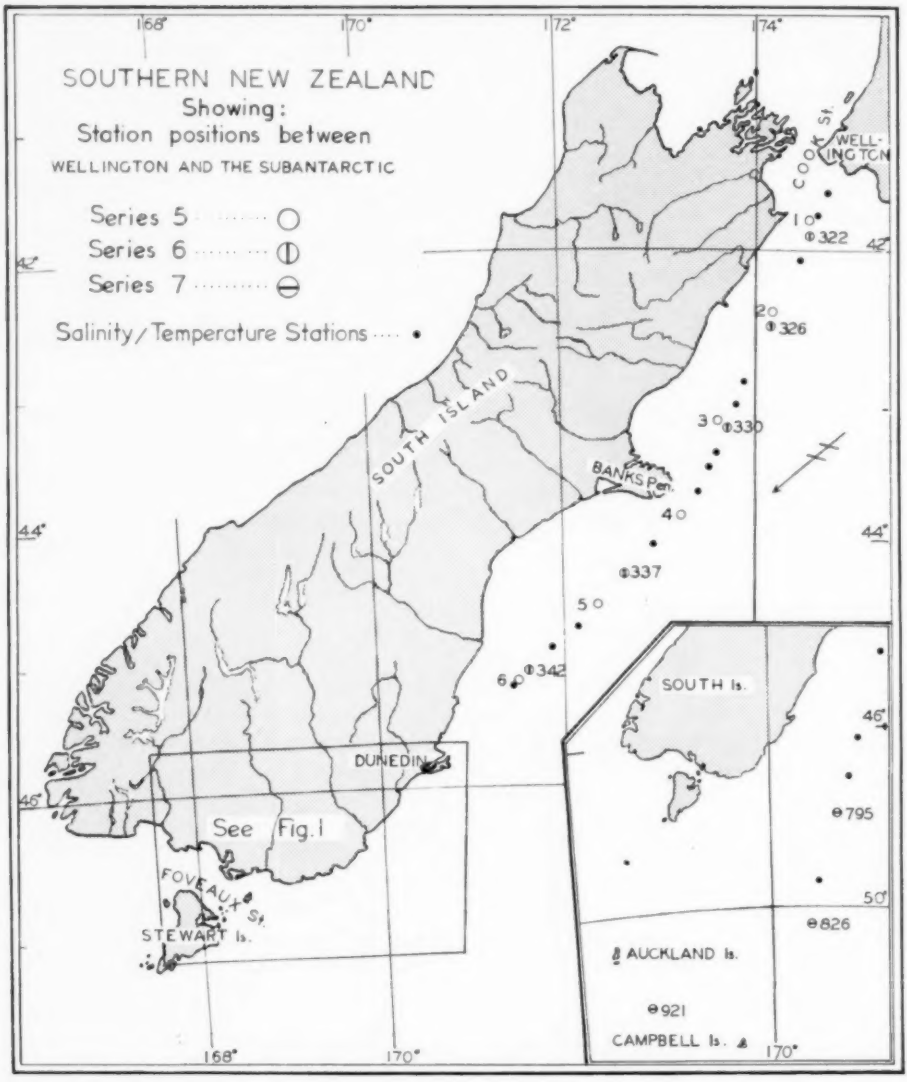


FIG. 2. Temperature/salinity, and plankton stations between Wellington and Dunedin in January (1–6), and March (320–343), 1951. The arrow shows the course of the ship which took the surface thermograph trace in Figure 4*b*. The approximate position of the subtropical convergence is shown by the two bars crossing the shaft.

INSET: Temperature/salinity and plankton stations between southern New Zealand and Auckland and Campbell islands, November 1951.

Only plankton stations are numbered.

TABLE 2
GENERAL PROPERTIES OF WATERS IN THE SUBANTARCTIC, AND OFF EASTERN AND SOUTHERN NEW ZEALAND*

WATER BODY	SALINITY, °/₀₀	TEMPERATURE, °C.
Of Subantarctic Origin		
i. cold subantarctic	34.0 to 34.3	8.2 to 10.9
ii. warmed subantarctic	34.3 to 34.7	11 to 13.0
Of Subtropical Origin	35.0 to 35.5	13 to 17.5 plus
Coastal	— up to 35	13 to 16 plus

* The values listed are derived from the present sampling, but they approximate those given by Deacon (1937) for waters of subantarctic and subtropical origins.

strated that for the particular local conditions, each is largely confined within certain ranges of salinity and temperature (except possibly where mixing is taking place), and that each occurs in conjunction with species which can be stated as undoubtedly resident in the water characterised by those properties. They are thus useful indicator species under the local conditions.

To cover the conditions which may occur in mixed waters it is necessary that indicator species are selected as far as possible to include a range of adaptabilities. To this end more than one species is desirable from each water body. Further, several species may provide additional information through their variable reactions. For example, an adaptable species may maintain an association with a mixture of particular waters whereas a less adaptable one would not.

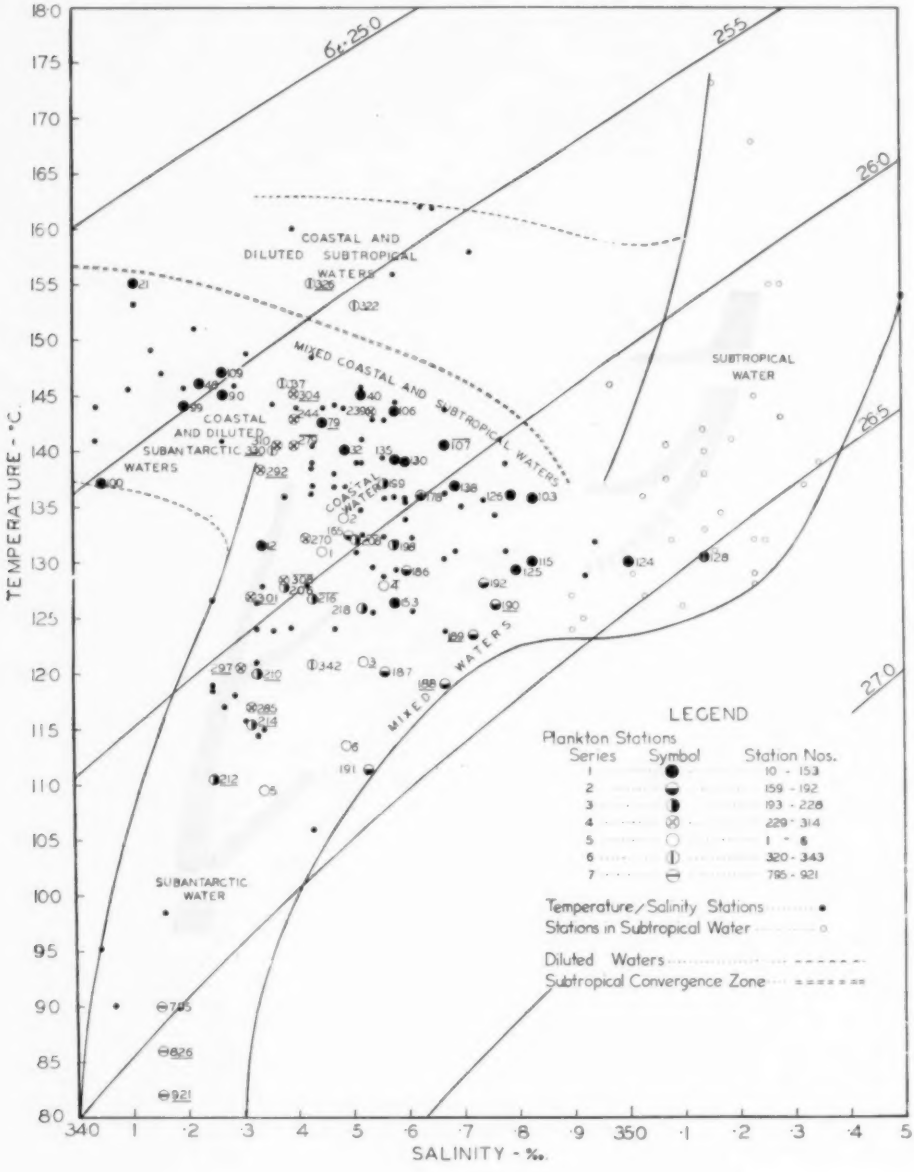
Frequent short plankton tows, with corresponding numbers of hydrographic samples, might well provide a better index to the overall surface conditions in an area than fewer hydrographic samples and fewer, but longer, tows. The latter may increase the quantity of a catch, but may decrease the relative accuracy with which the biologic sample can be related to the physico-chemical conditions. This would apply especially where steep gradients may exist, as for example in mixing waters. The geographic distributions of indicator species selected from the three-minute tows of this survey are found to closely coincide with the geographic distributions of their respective waters. This general accord suggests that, although surface tows may vary quantitatively and qualitatively between one time and place and another, the present procedures have largely met the requirements for this type of study.

Collections were made as opportunity permitted. As a consequence two features possibly affect the distribution of species in the T–S–P diagrams, namely, diurnal migration of species and the asynoptic nature of the collections.

The effects of diurnal migration have been analysed in some detail. (Times of stations are given in Table 4. In this table, and in Fig. 3, stations are divided into those occupied during daylight, at night, and between dawn and sunrise, and between sunset and dark.) As would be expected, the numbers of species and of specimens captured increased at night (Table 4). It was thought that variations of this nature might render the T–S–P diagram of less value in the selection of indicator species, and, more especially, for reliably correlating their distributions with hydrological conditions. The fact that several species form an indicator group has some bearing. Thus, if the suspected adverse effects of diurnal migration on distribution were to be realised, all species of a group would have to react similarly at the one time. Occasions will arise when all species of a group could, for example, be absent from the surface at the same time. These occasions appear to affect group-distribution patterns in the diagrams

only in details, as discussed below.

The analysis has shown that all series of stations contained night tows and in all, except Series 1, at least some of these were consecutive. In addition, some species from the groups were captured in both day and night hauls. Two important facts were also demonstrated. First, fewer night than day tows are



needed to produce a T–S–P diagram from which the distribution of the species group can be related to the hydrological conditions. Second, and the more important, is that in the majority of instances, *those species which were taken in daylight occurred in similar conditions of temperature and salinity to the same species taken at night*. In other words, when a species was collected in day and night tows, it occurred almost only in the environmental conditions which were acceptable. This is reflected in the cohesion of the species' distributions in each of the groups in the T–S–P diagrams. Therefore, day tows serve to supplement night tows from a distributional point of view in the diagrams, and it is believed that data from both may justifiably be used in their construction. It has been found preferable to base interpretations of distributional relationships on the species' groups because diurnal migration may be affecting detail. To guard against the possible adverse effects which might accrue, it would be desirable to occupy future stations at comparable times, and preferably at night.

In T–S–P diagrams planktonic groups, or species, are shown independently of their times of capture. Therefore, occurrences of either individual species, or groups of species, can be directly related only to the environmental conditions in which they were captured, and to the species' composition at other stations. The species, and through them, the species' groups, will react to environmental changes (if of sufficient magnitude), but when these occur is not important in the T–S–P diagram. It is possible, therefore, to utilise asynoptically collected data in the T–S–P diagram. When species or groups of species are considered in relation to the geographic distribution of the water properties then it becomes essential that as near synoptic series as possible are utilised. Nevertheless, it is believed that even for the T–S–P diagram, the nearer the approach is to synoptically made collections (as, for example, Series 4 to 6), the more reliable will be interpretations from the diagrams.

Pickford (1952: 209) has plotted the occurrences of *Vampyroteuthis infernalis* in relation to density as well as salinity and temperature. She quotes a suggestion that the distribution of this species is determined by its being "passively caught in a layer of constant density. . . ." Because of this suggestion, densities are plotted in Figures 3 and 10. It appears from Figure 10, however, that species may occur over a wide range of densities. It would appear, therefore, that this factor has little if any control over the distribution of surface zooplankton in the area of sampling.

WATERS INFLUENCING SOUTHERN AND EASTERN NEW ZEALAND

The surface waters are described as being of subtropical origin in the northern half and of subantarctic origin in the southern half of eastern New Zealand (Deacon, 1937; Garner, 1954). To the west, and lying north of an ill-defined subtropical convergence zone (Garner, *loc. cit.*) is Tasman Sea water. It is believed to move in an east-going drift towards New Zealand (Deacon, *loc. cit.*). On approaching the west coast of South Island the bulk of the water seems to be deflected northwards while some is thought to move southward and penetrate towards Foveaux Strait and Stewart Island (Deacon, Garner).

FIG. 3. T–S diagram of surface waters, southern and eastern New Zealand. Stations at which plankton was collected are differentiated from those where only salinities and temperatures were taken. Stippled arrows indicate the direction of water movements within the diagram, as deduced from the distribution of properties and the form of the water envelope (and as later confirmed by the plankton distribution). An underlined station number, e.g., 212, indicates a night tow; an overlined station number, e.g., 216, indicates a station occupied at dawn or dusk. An unmarked station is one occupied in daylight.

NOTE: The shape of this diagram superficially resembles that of the area in which samples were taken, but it is not a reproduction of the geographic area in another form.

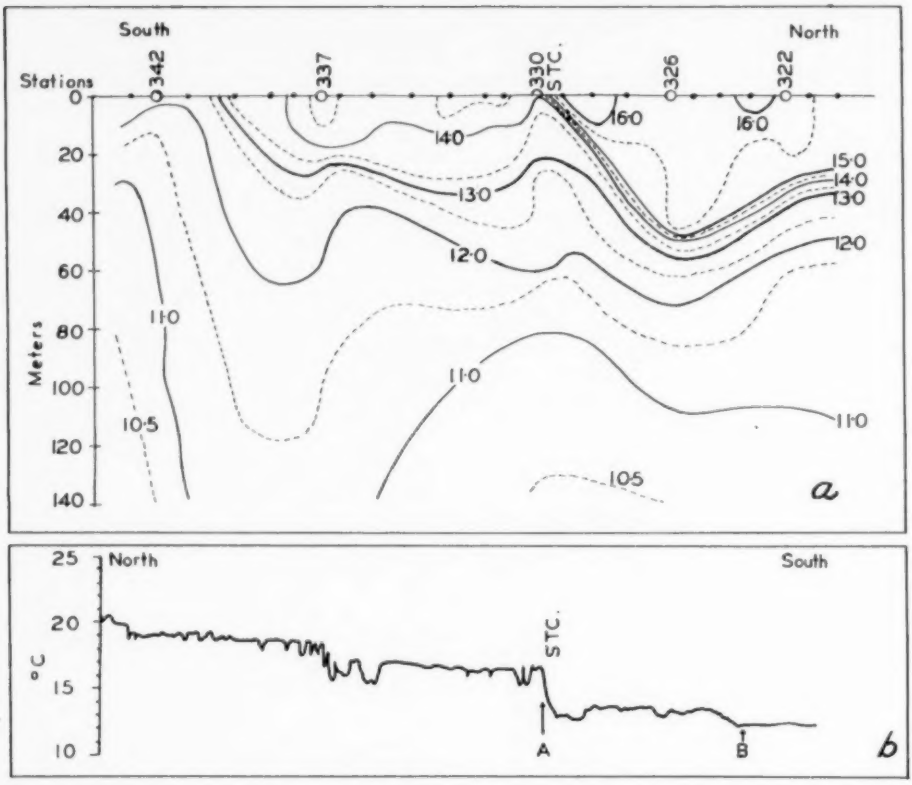


FIG. 4. *a*. Section to 140 m. between Wellington and Dunedin, March 21, 22, 1951. STC = position of subtropical convergence. Stations indicated by a circle are those at which bathythermograph casts were made; surface temperatures were taken at positions marked by dots.

b. Surface thermograph trace between 37° 32′ S. and 178° 29′E. and Dunedin, mid-April, 1951. STC = position of subtropical convergence in 43° 24′S. 174° 34′E. (position A) distant 45 mi. and bearing approximately 96° from Station 330.

Few detailed data are available concerning the properties of the eastern central and southern Tasman Sea water.[2] That it is warmer and more saline than water of subantarctic origin is demonstrated by the temperatures and salinities of surface samples from the west of North Island between Wellington and North Cape (small open circles, Fig. 3). These data are of winter (July) conditions and consequently temperatures are low in comparison with the rest of the stations, which are summer stations. The temperature ranges between 12.5° and 17.5°C. and the salinity between 35.0 and 35.5°/₀₀, values which are within those described for subtropical waters by Deacon (1937). For this

[2] Since this paper went to press, Rochford, D. J. (1957) has published an account of the waters of the Tasman Sea. He indicates that for the area west and south of South Island, New Zealand, subantarctic water exerts the main influence at all times. However, his data do not preclude the possibility that during spring and summer months some influence from warm Tasman Sea water (in part, my "water of subtropical origin") may penetrate southwards along the west coast towards Foveaux Strait. See his figure 25b.

TABLE 3
SPECIES' GROUPS, AS DETERMINED FROM THE T–S–P DIAGRAMS, AND THE WATERS OF WHICH THEY ARE INDICATORS

SPECIES' GROUP	WATER
Subantarctic	Water of Subantarctic origin
i. Southern Subantarctic species	from 8°C.
ii. Northern Subantarctic species	11°C. and higher
Subtropical Species	From, or due to, the influence of subtropical water
Coastal Species	Coastal water—an admixture of subantarctic, subtropical and fresh waters

reason, and for lack of any published evidence to the contrary, the Tasman Sea water and the waters northward of the subtropical convergence to the east of New Zealand are considered together as "water of subtropical origin" in this study. Whether in fact the physical and faunistic properties of the two areas will prove to be identical, or nearly so, has yet to be demonstrated. For the purpose of the present investigation the T–S characteristics of this water are included in Figure 3 for two reasons. First, they provide a contrast across the subtropical convergence with the water originating in the subantarctic; second, they delineate the mass from which the warm saline water (and a warm-water fauna) that influences southern and north-eastern South Island is being derived.

Subantarctic (West Wind Drift) water moves mostly toward the east, but with a northerly component. It has a strong influence on the waters of southern and eastern South Island (Garner, 1954) and perhaps also in some measure on those of the west coast. Some is also believed to pass into Foveaux Strait from the west. The temperature at Station 921 (Fig. 2) was 8.2°C., and it increases northwards to about 13°C. at the convergence. Salinity ranged between 34.0 and 34.3 °/₀₀ in the colder waters and 34.3 and 34.7 °/₀₀ in the warmer (northern) waters. Such values are within those described for subantarctic water by Deacon (1937). The properties of these waters are summarised in Table 2 and their relationships illustrated in the T–S diagram, Figure 3.

Waters of subtropical and subantarctic origins meet in the subtropical convergence, a zone usually described as of variable width which is believed to migrate northwards in winter, southwards in summer. The existence of the convergence eastwards of New Zealand is undoubted, from evidence discussed by Deacon (1937) and Garner (1954). Evidence from the present survey indicates that it was crossed twice, with biological and hydrological samples being obtained during the first traverse. Data from surface waters from the cruise of March 21–22, 1951 (see Series 6, pp. 47, 48, and Figs. 4*a*, 19*b*, 20*b*), show that near Station 330 there was an abrupt increase northwards of 2°C. and of 0.3 to 0.4 °/₀₀ salinity (over subantarctic salinities as at Stations 341, 342). The section constructed on the basis of bathythermograph records to 450 feet (approximately 138 m.) from between Wellington and Dunedin (Fig. 4*a*) shows that towards the north cool water was submerged beneath a layer 35 to 60 m. deep of warmer water. Immediately north of Station 330 this cool water reaches the surface. South of Station 330, and including Station 337, is a second body of warm water which is of coastal origin (Figs. 19*b*, 20*b*) and which overlies, and is mixing with, subantarctic water. On the second crossing on April 18, a surface thermograph trace (Fig. 4*b*) recorded a temperature drop from 16.8° to 12.8°C. in a position approximately 45 miles seaward on a bearing of 96° from Station 330 (Fig. 19*b*). These data are typical of those associated with a convergence of warm and cold waters, and it is believed they are attributable to the subtropical convergence. This would fit in with Garner's interpretation of these and other data, and, if so, the crossings herein discussed were of the southern extremity of a south-going tongue of subtropical water which was

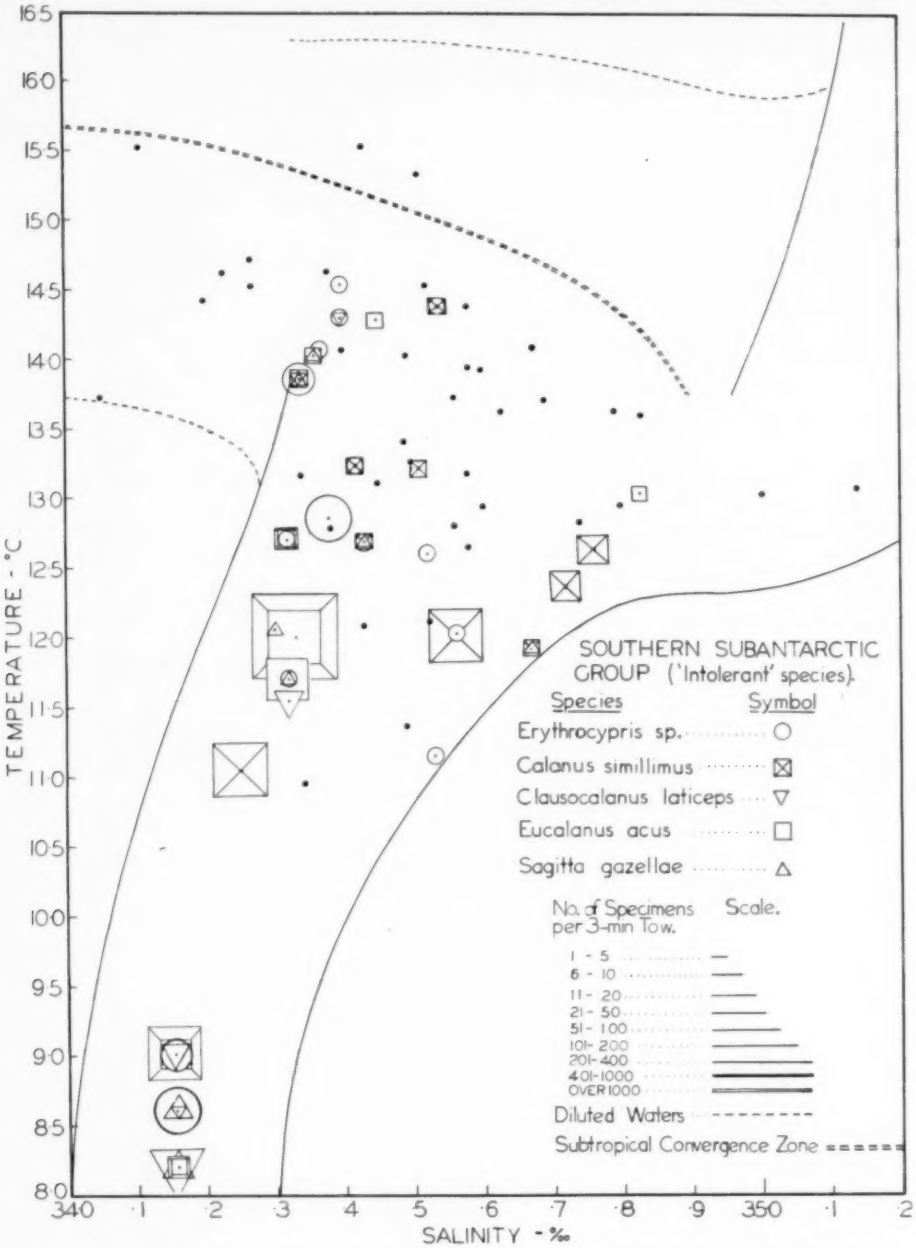


FIG. 5. The distribution in the temperature–salinity–plankton (T–S–P) diagram of Southern Subantarctic species which show a lack of adaptability toward coastal water through a marked reduction in the numbers taken from it. Water envelope as in Figure 3. Plankton stations at which no specimens were collected are shown by ●

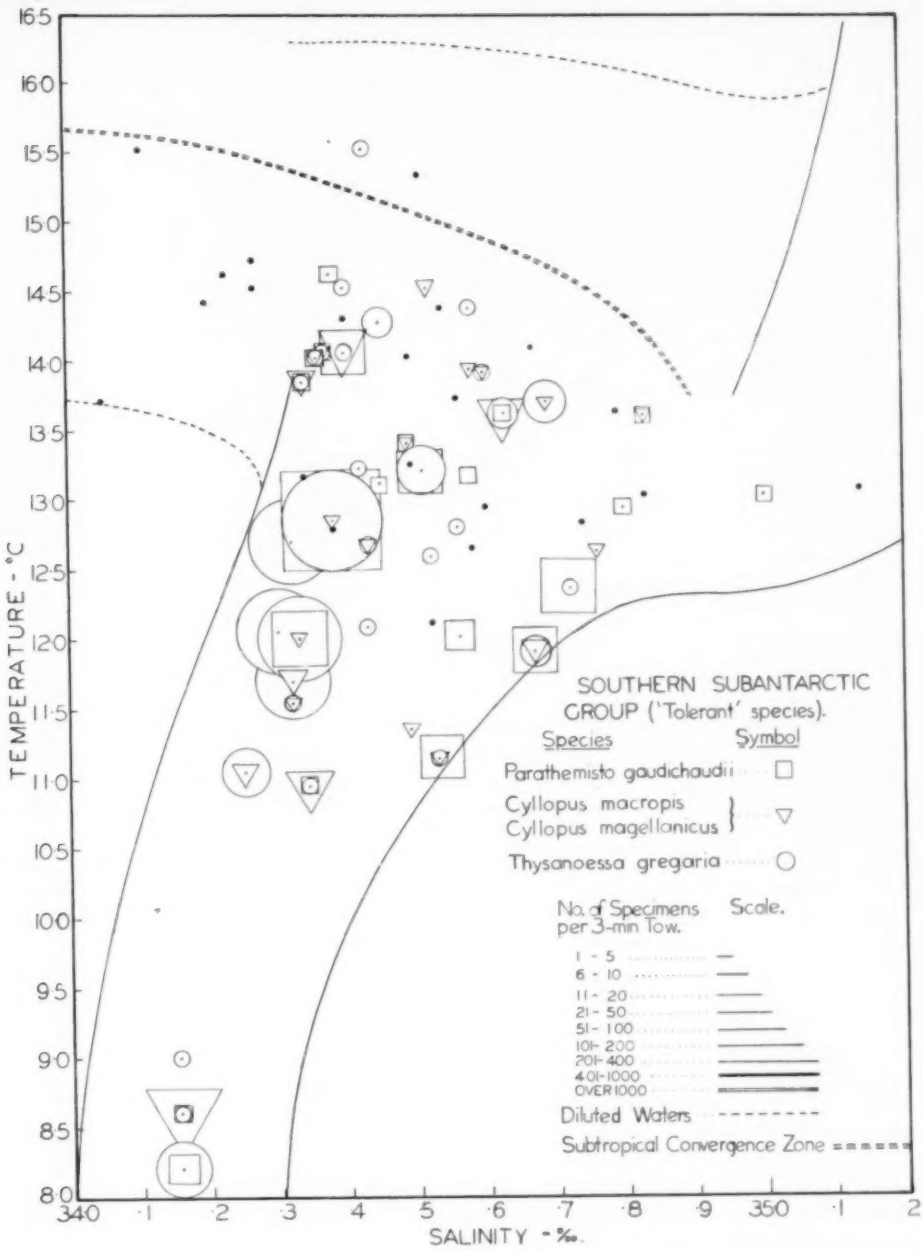


FIG. 6. The distribution in the T–S–P diagram of Southern Subantarctic species which are comparatively more widespread in (i.e., more "tolerant" of) coastal water. The numbers taken are higher in the coastal water than for the "Intolerant" species shown in Figure 5. Plankton stations at which no specimens of the group were taken are shown by ●

penetrating down the east coast—an extension of the East Cape Current (see Garner 1954, also his fig. 4*a*). That the data are in fact attributable to crossing the convergence is borne out to a considerable degree by the biological evidence.

Coastal water appears from Figure 3 to be an admixture of fresh water runoff and water of subtropical and subantarctic origins. Subantarctic water is of lower salinity than the water of subtropical origin and will dilute it; both of these waters and their mixtures will be diluted by fresh water. The salinity of coastal waters ranged from less than 34 °/₀₀ (not shown in Fig. 3) up to about 35 °/₀₀, and depends in part on which oceanic water predominates at a station, and on the proportion of fresh water in the coastal water mixture. The temperature ranged between 13° and 16°C., which is intermediate between those of waters of subtropical and subantarctic origins.

In the T–S diagram (Fig. 3) the water envelopes have been drawn arbitrarily to include all points entered. Solid lines indicate those water masses identifiable from the present data; dashed lines are indicative of dilution of the waters from these masses. The double dashed line signifies the subtropical convergence and separates all stations occupied to the south of it from those to the north. The proper extent of the convergence cannot be shown because the low winter temperatures of the water of subtropical origin permit the coolest samples from this water to be located in the summer temperature range of the coastal–subtropical mixture. Because of this, and because no stations crossed the convergence clear of the influence of coastal water, no position for the subtropical convergence between uncontaminated waters is shown in the diagram.

From the distribution of properties in the T–S diagram and from its form, general movements of both subtropical and subantarctic waters towards coastal water can be deduced. There will be mixing between these (and with fresh water) and this is represented in the region of extreme salinity variation in the temperature range of about 13° to 15.5°C. Confirmatory evidence on water movements and especially those concerning mixing areas is to be derived from the distribution and interrelationships of the several groups of indicator species. In Figure 3, the stippled arrows show the general water movements as deduced from the T–S diagram, while in Figure 10 the movements as demonstrated by the planktonic distribution are illustrated. There is a general similarity.

SPECIES' GROUPS IN RELATION TO WATERS IN THE AREA

Four groups of species have been selected as representative of the zooplankton resident in the waters of the area of sampling (Tables 3, 4). There is one group from each of the coastal and subtropical waters, and two from water originating in the subantarctic. One of the subantarctic groups represents those species occurring predominantly in the colder waters and for convenience called the "Southern" Subantarctic Group; the other has been selected from those species occurring in water of subantarctic origin which has been warmed in its progress northward, namely, the "Northern" Subantarctic Group (see pp. 31–33).

The species and the species' groups are listed in Table 4, together with the numbers of specimens captured and the stations at which they were taken.

The degree to which the association of species in each of the groups is maintained in their normal environment, and when they are carried into abnormal conditions, is summarised in Figures 5 to 9 and is discussed below.

Southern Subantarctic Group

Stations 795, 826, and 921 (Fig. 2) lie within the field of cold subantarctic water as defined earlier, and appear to be removed from the influence of water of subtropical

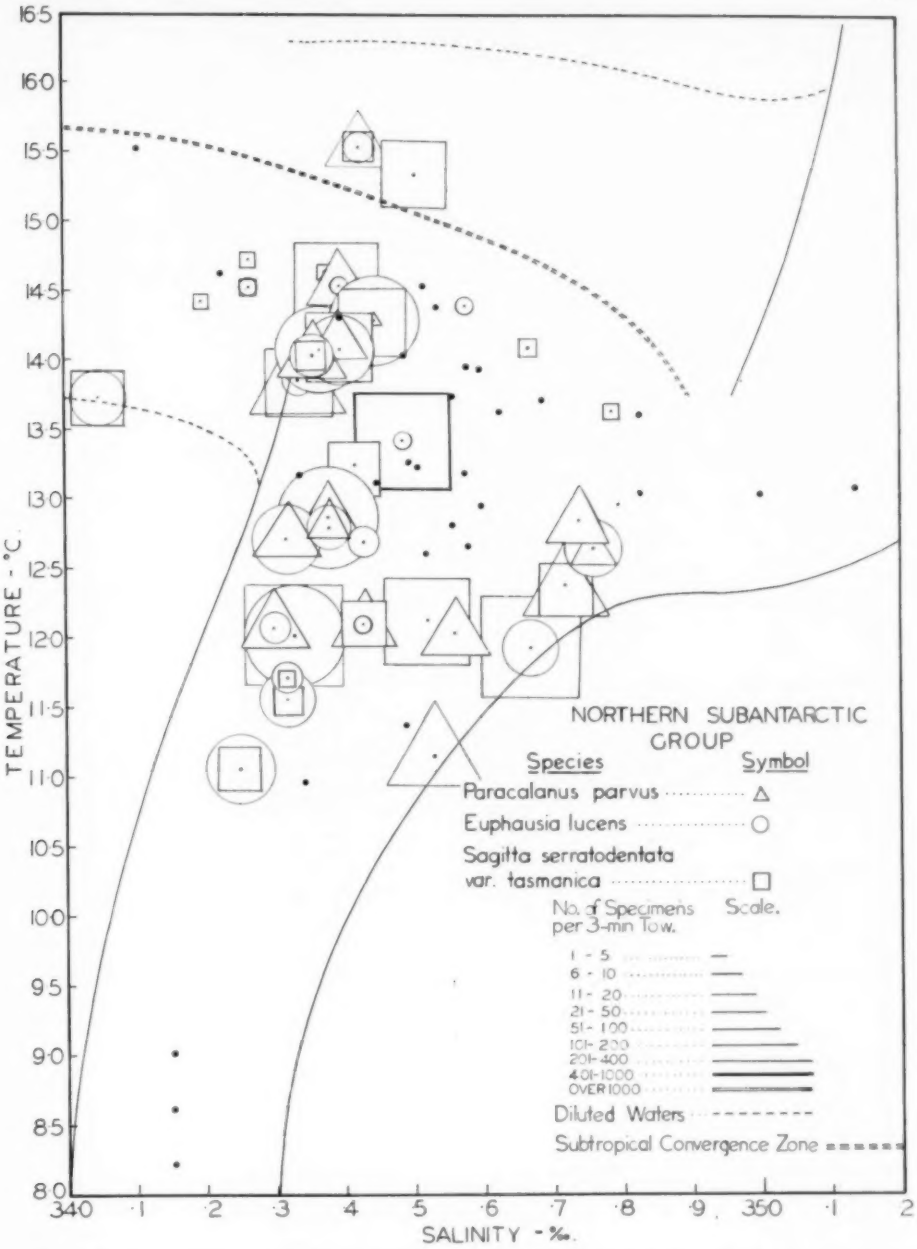


FIG. 7. The distribution of Northern Subantarctic species in the T–S–P diagram. Large numbers were taken. The species are confined to the northern, warmed subantarctic water, but extend into coastal water in strength in two areas where the subantarctic water is intruding into and mixing with, coastal water. Plankton stations at which no specimens of the group were taken are shown by ●

TABLE 4
THE PLANKTON STATIONS, THEIR TIMES AND DATES, AND THE SPECIES AND GROUPS COLLECTED AT EACH

STATION NO.	TIME OF DAY† (HOURS)	SERIES		SOUTHERN SUBANTARCTIC									NORTHERN SUBANTARCTIC			SUBTROPICAL				COASTAL					
		Dates	No.	"Intolerant"					"Tolerant"																
				Erythrocypris sp.	*Clausocalanus laticeps*	*Eucalanus acus*	*Calanus similimus*	*Sagitta gazellae*	*Paralbemisto gaudichaudii*	*Cyllopus magellanicus*	*Cyllopus macropis*	*Thysanoessa gregaria*	*Paracalanus parvus*	*Euphausia lucens*	*Sagitta s. tasmanica*	*Sapphirina* spp.	*Hyperoche mediterranea*	*Iblea magalhanica**	*Thalia democratica**	*Tenagomysis macropsis*	*Tenagomysis tenuipes*	*Paralbemistо gracilipes*	*Paralbemistо australis*	*Nyctiphanes australis*	*Oikopleura dioica*
1	1605.D																								
2	2000.D								1	1				3	607										
3	0005.N	3–4.I.51	5												111						7				
4	0400.O											4											3		
5	0800.D								4	25		4													
6	1200.D									1															
12	1200.D																								86
21	1355.D																	7							15
32	1624.D																	3							86
40	1810.D									2								334			8				312
48	2000.D																8	17		JUV.					
79	2210.N					1						8		100+	92		52	51		400+	9	12	5	256	
90	0945.D													3			11	25						1	
99	0945.D														1		1								
100	2030.D													40	24		24			3000	292		8	26	
103	1010.D								1	1											3				
106	1605.D	5–6 to 24.I.51	1									2		1			1			1					
107	2105.O														1		2	62		55	6	1	1	3	
109	1120.D														4			4							
115	1125.D					1																			
124	1250.D								1													61	6		
125	1515.D								1									6		1		46	8	2	
126	1615.D														2			37							
128	1830.D																	27					3		
130	0925.D									3		3						6				3	3		
135	1410.D									3													1		

TABLE 4 *Continued*
THE PLANKTON STATIONS, THEIR TIMES AND DATES, AND THE SPECIES AND GROUPS COLLECTED AT EACH

STATION NO.	TIME OF DAY † (HOURS)	SERIES		SOUTHERN SUBANTARCTIC									NORTHERN SUBANTARCTIC			SUBTROPICAL				COASTAL					
		Dates	No.	"Intolerant"					"Tolerant"																
				Erythrocypris sp.	*Clausocalanus laticeps*	*Eucalanus acus*	*Calanus simillimus*	*Sagitta gazellae*	*Parathemisto gaudichaudii*	*Cyllopus magellanicus*	*Cyllopus macropis*	*Thysanoessa gregaria*	*Paracalanus parvus*	*Euphausia lucens*	*Sagitta s. tasmanica*	*Sapphirina* spp.	*Hyperoche mediterranea*	*Ibla magalhanica**	*Thalia democratica**	*Tenagomysis macropsis*	*Tenagomysis tenuipes*	*Parathemisto gracilipes*	*Parathemisto australis*	*Nyctiphanes australis*	*Oikopleura dioica*
138	1915.D									3		13						347		2		8	1	11	
153	1045.D																	2							
165	1300.D																	2						4	
178	1725.D								4	27		6						6				57	6	1	
186	1715.D																								
187	1915.D	29.I. to 1.II.51	2	1			30		13				60										1		
188	2300.N						2	1	28	8		8		48	208						9				
189	0125.N						7		80			5	140		36						112	184	48	201	
190	0335.N						10			4			16	40										1	
191	0630.D			1					17	4		1	240												
192	1430.D												72												
198	1700.D			1					1													3			
199	1845.D																								
206	1715.D												16	19											
208	2020.O	5–13.II.51	3				2		46			13										1	1		
210	2230.N					27	144		88	1		195		336	344										
212	0130.N						25			4	2	16		85	13									1	
214	0300.N				7						2	4		32	6										
216	0500.O			2			3	1			3	2		9											
218	0630.D			1								1													
239	1250.D			2			1																		
244	1520.D			5	2																				
270	1815.D			3			1					1			41										
279	2010.O								37	36		1	21	70	87								12	3	

TABLE 4 *Continued*

THE PLANKTON STATIONS, THEIR TIMES AND DATES, AND THE SPECIES AND GROUPS COLLECTED AT EACH

STATION NO.	TIME OF DAY† (HOURS)	SERIES		SOUTHERN SUBANTARCTIC									NORTHERN SUBANTARCTIC			SUBTROPICAL				COASTAL					
		Dates	No.	"Intolerant"					"Tolerant"																
				Erythrocypris spp.	*Clausocalanus laticeps*	*Eucalanus acus*	*Calanus similimus*	*Sagitta gazellae*	*Paratheniisto gaudichaudii*	*Gyllopus magellanicus*	*Gyllopus macropis*	*Thysanoessa gregaria*	*Paracalanus parvus*	*Euphausia lucens*	*Sagitta s. tasmanica*	*Sapphirina* spp.	*Hyperoche mediterranea*	*Ibla magalhanica**	*Thalia democratica**	*Tenagomysis macropsis*	*Tenagomysis tenuipes*	*Parathemisto gracilipes*	*Parathemisto australis*	*Nyctiphanes australis*	*Oikopleura dioica*
285	2200.N			2		16		3		8		67		6	5										
292	0015.N	8–9.III.51	4	7	1	2		1	1	10		3	288	8	55				243				1	249	
297	0205.N							3				200	100+	7											
301	0315.N			1		1	1					119	100+	87					6						
304	0423.N			1								1	100+	3	104				396						
308	0550.O			14					376	1		496	100+	236							10	24			
310	0630.D			3					5	1				115							1	15	3		
322	1630.D														55	165			1250		2	1			
326	2035.N											3	100+	6		31		11	826		1		14	9	
330	0030.N	21–22.III.51	6			1			3	1		5	100+	21	8	1									
337	0715.D								1						4								94		
342	1217.D											4	100+	4	14										
795	1900.D			8	8	9	23					1													
826	0300.N	13–17.XI.51	7	12	3			10	4	143		1													
921	0300.N				40	3	3	9	8			30													

* Combined totals of solitary and aggregate forms shown separately in Figure 8.
† D = daylight stations; N = stations at night; O = stations from dawn to sunrise, or sunset to dusk.
\+ Signifies larger numbers of specimens than were counted.

origin. Species taken at these stations may be regarded as resident in such subantarctic water. Accordingly the species of the Southern Subantarctic Group have been selected from those collected at these stations.

Nine species have been selected. *Erythrocypris* sp., *Clausocalanus laticeps* Farran, and *Sagitta gazellae* Ritter-Zahony were present in small numbers, *Eucalanus acus* Farran in moderate numbers, and *Calanus simillimus* Giesbrecht was often very common, preponderantly as a Stage V copepodite. *Clausocalanus laticeps* and *E. acus* are both described as typically cold-water species (Farran, 1929; Hardy and Gunther, 1935) and stocks of *S. gazellae* are demonstrated as residing in antarctic and subantarctic waters by David (1955). *Calanus simillimus* is only to be captured from the southern waters (Vervoort, 1951). The numbers of these five species were noticeably reduced in coastal and mixed waters, which possibly indicates a lack of adaptability to the changed conditions. Consequently they have been distinguished as "Intolerant" species (Fig. 5). *Parathemisto* (*Euthemisto*) *gaudichaudii* (Guer.) and *Thysanoessa gregaria* Sars occurred commonly, but *Cyllopus macropis* (Bovallius) and *C. magellanicus* Dana were present in smaller numbers. *Thysanoessa gregaria* was discussed on page 17. *P. gaudichaudii* is a fairly widespread species in the colder waters of northern and southern hemispheres, while *Cyllopus* spp. have been recorded only from the colder southern waters (Stebbing, 1888; Barnard, 1930; Hurley, 1955; Hardy and Gunther, 1935). Larger numbers of these species penetrate into coastal waters, which suggests a greater tolerance towards altered conditions than was apparent among the "Intolerant" species; they are accordingly distinguished as "Tolerant" species (Fig. 6). Both "Tolerant" and "Intolerant" species belong in the Southern Group.

In the T–S–P diagrams Southern Subantarctic species are in continuous distribution, in moderate to high numbers, throughout water of subantarctic origin. All of the species occur as well in coastal water, but the numbers of specimens collected decrease with modification of the environmental conditions as mixing progresses between the subantarctic and coastal waters. This is especially so of the "Intolerant" species. Dilution by fresh water (Stations 99, 90, 48, 109) and, to a lesser degree, increase in salinity (Stations 126, 103, 124) appear to restrict the "lateral" spread of species in the diagrams although much of their apparent effects may be due to the stations having been occupied in daylight. Rising temperatures are less restrictive. Most of the species were taken throughout the range sampled, but much less commonly at the higher temperatures, even in hauls made at night.

Transfers of species from subantarctic to coastal waters were largely concentrated about three groups of stations, namely 292, 330, 310, 304, 79, 40, and 189, 190, 125. Subantarctic species also extend, in small numbers, through Stations 218, 4, 198, 208, to 178, 138, and 130. The stations of these three aggregations will be referred to subsequently when it will be found that they were situated in mixing waters (see Figs. 3, 10).

Northern Subantarctic Group

The species selected for the Northern Subantarctic Group were confined to that warmer water (i.e., 11°C. and higher) which is believed to have originated in the higher latitudes of the subantarctic. None was present in the colder waters at Stations 795, 826, or 921 (Fig. 2). Three species have been selected, namely, *Sagitta serratodentata* Krohn var. *tasmanica* J. M. Thomson, *Paracalanus parvus* (Claus), and *Euphausia lucens* Hansen.

Sagitta serratodentata has been described as "cold tolerant," while the variety *tasmanica* is reported to inhabit waters of 11° to 17°C. (Thomson, 1947). John (1936) describes *E. lucens* as predominantly a northern subantarctic species occurring most frequently between 12° and 14°C., which confirms Tattersall's

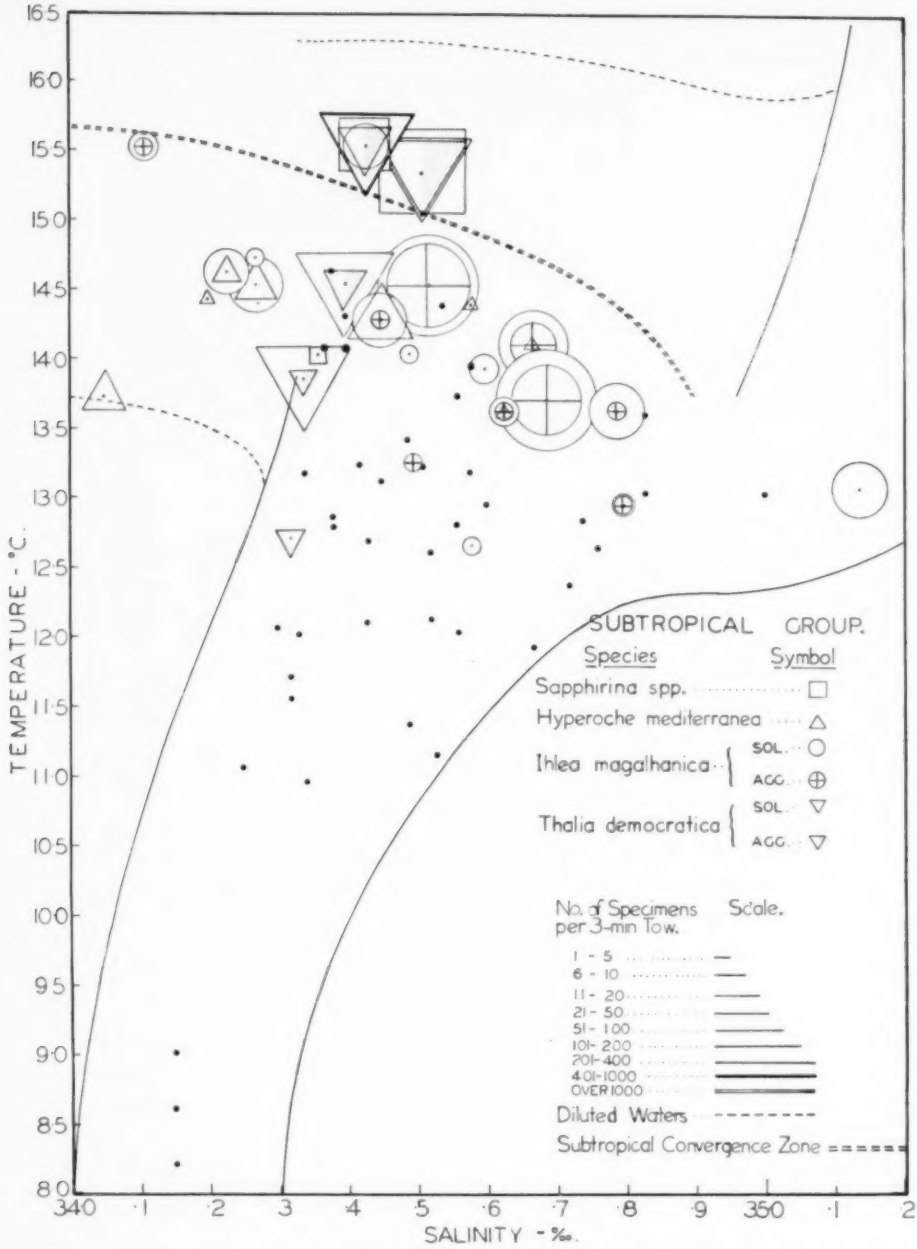


FIG. 8. The distribution of Subtropical species in the T-S-P diagram. Species are almost confined in the warmest water. Plankton stations at which no specimens of the group were taken are shown by ●

(1924) appreciation of its distribution. Thus the distribution of these species as shown in the T–S–P diagram (Fig. 7) agrees with previous accounts. The distribution of *P. parvus* is restricted to that recorded previously (see p. 17).

The distributions of the species and the numbers captured relative to temperatures and salinities are shown in Figure 7. It is evident that the numbers taken were often large. All species were strongly represented at Stations 292, 330, 310, 79, etc., and 189, 190, (referred to as being in mixed waters in the discussion of the Southern Subantarctic Group), but are present only as rarities, or are absent from collections at other stations in coastal-subtropical waters. Reduced numbers were taken at Stations 212 and 214 in colder waters. As these were night stations this reduction may be a reflection of the effects of the lower temperatures. At some other stations in these colder waters, e.g., Stations 5, 191, 6, specimens were absent or rare, but this may be a result of the stations being occupied in daylight.

Not only do the Northern Subantarctic species inhabit the comparatively warmer water of subantarctic origin, but they can penetrate into warm mixed waters in larger numbers than any of the Southern Group of species. This may be consequent on their adaptation to higher temperatures in their more usual habitat. According to John (1936), there is a gradual amelioration of conditions, with changes in the composition of the planktonic fauna to correspond, as one proceeds from colder to warmer northern waters in the subantarctic. Therefore the abrupt transition suggested by the convenient subdivision of the species into Northern and Southern Subantarctic Groups probably over simplifies the faunal distribution. Further sampling at temperatures lower than 11°C. may demonstrate a gradual decrease in the frequency of occurrences and in the number of species taken of the Northern Subantarctic Group—a decrease which would accord with John's views. However, such would not necessarily detract from either the Southern or Northern groups of species as indicators of the particular conditions for which they have been selected.

Subtropical Group

The species of the Subtropical Group have been selected on the basis of their previous distributional records. Although detailed sampling is required in those New Zealand waters which are beyond doubt of subtropical origin in order to demonstrate that the species originated there, it is believed that they are typically of the subtropical population. The species selected are *Sapphirina* sp., *S. angusta* Dana, *S. gemma* Dana, *S. sali* Farran, and *S. pyrosomatis* Giesbrecht (see Wilson, 1932), *Ihlea magalhanica* Apstein, *Thalia democratica* Forskal (see Thompson, 1942, 1948), and *Hyperoche mediterranea* Senna (Stephensen, 1924, Hurley, 1955). Of these, *H. mediterranea* did not occur at Stations 322 and 326, and *Sapphirina* spp. were taken only at these stations.

The wide range of salinities (Fig. 8) over which these species are taken points to their tolerance in this regard. On the other hand, the species maintain a close association with the warmest water and only exceptionally are specimens taken outside of it. The group thus strongly contrasts with the two Subantarctic groups.

The species of this group are normally associated with subtropical water. In this survey they occur largely in the warmest water (Fig. 8), and therefore it is suggested that this water is of, or is being influenced by, water of subtropical origin. Except for Stations 322 and 326, the majority of the collections of the Subtropical species were from stations of Series 1 (see Figs. 1, 3), mostly within Foveaux Strait, i.e., within the area expected to be most strongly influenced by any eastward flow of water from subtropical sources. The few other occurrences of the species usually are associated with coastwise extensions of the subtropical influence.

It may be coincidental that the Subtropical species have proved adequate to indicate the waters of subtropical origin from both east and west of New Zealand. If further investigation shows that the faunas are dissimilar, separate indicator groups would probably need to be established for the waters of each of these areas.

Coastal Group

Species indigenous to coastal waters must necessarily be tolerant of the considerable fluctuations in temperature and salinity which may occur in these waters. The species of the Coastal Group are distinguished from the Subtropical Group by occurring over a much wider range of temperatures (Figs. 8, 9). Six species have been selected, namely *Tenagomysis macropsis* Tattersall, *T. tennipes* Tattersall, *Parathemisto* (*Euthemisto*) *gracilipes* Norman, *P.* (*E.*) *australis* Stebbing, *Nyctiphanes australis* Sars, and *Oikopleura dioica* Fol. *Nyctiphanes australis* is a recognised coastal species (Sheard, 1953), as is *O. dioica* (Thompson, 1948). *Tenagomysis* spp. have been confined almost completely to neritic conditions (Tattersall, 1918, 1923; Bary, 1956). *Parathemisto australis* has been collected previously only in coastal areas (Stebbing, 1888; Barnard, 1930), which is true of the present material (Hurley, 1955). *Parathemisto gracilipes* occurred in similar localities to, and was often captured with, *P. australis*, although the literature describes it as an oceanic species. Of these species only one specimen of *N. australis* was captured in water of unquestioned subantarctic origin (Station 212, Fig. 9), presumably as a stray. On the other hand, all species were present very commonly at stations where subantarctic water is believed to have been mixing with coastal water (Stations 292, 310, 330, etc., and Stations 189, 190, 125). A few specimens of *Parathemisto* spp. were taken at Station 322—suggestive of coastal water at the station. The occurrences of Coastal species at Stations 124 and 128 are not inconsistent. These stations lie in highly saline water which appears to be originating in a large shallow inlet on the north coast of Stewart Island (Patterson Inlet, Figs. 1, 12), and it is this water which locates the stations in the part of the diagram representing subtropical water (Fig. 3).

There is a general, but patchy, distribution of Coastal species throughout the coastal water, from high to low salinities and up to the highest temperatures. Nevertheless, they are almost completely absent from subantarctic water, even when it is contiguous with coastal water. It is believed that the species either are unable to survive being transferred from the coastal into subantarctic water, or that some physical process at the boundary between the waters prevents such a transfer (see pp. 48–49).

INTERRELATIONSHIPS BETWEEN SPECIES' GROUPS, AND TEMPERATURES AND SALINITIES

The interrelationships of the species' groups and their correlation with temperatures and salinities are shown in Figure 10. The groups are distinguished in the figure by hatching, and a subjective estimate of the abundance of each is indicated. The "area of chief concentration" is demarcated by lining-in and represents that portion of the diagram in which the bulk of each of the groups was captured.

As particular organisms are undoubtedly characteristic of particular waters, those instances where species from several waters are found together are believed to represent areas of mixing waters. Figure 10 illustrates that there are aggregations of stations (already referred to) from which large mixed catches were consistently made. Stations 292, 330, 310, 279, 304, 40, and 79 (refer also to Fig. 3) form one aggregation and Stations 189, 190, and 125 another. All four species' groups were present at most stations of the first aggregate, which indicates that the collections are from a mixture of the three waters. Subtropical species were absent from stations of the second

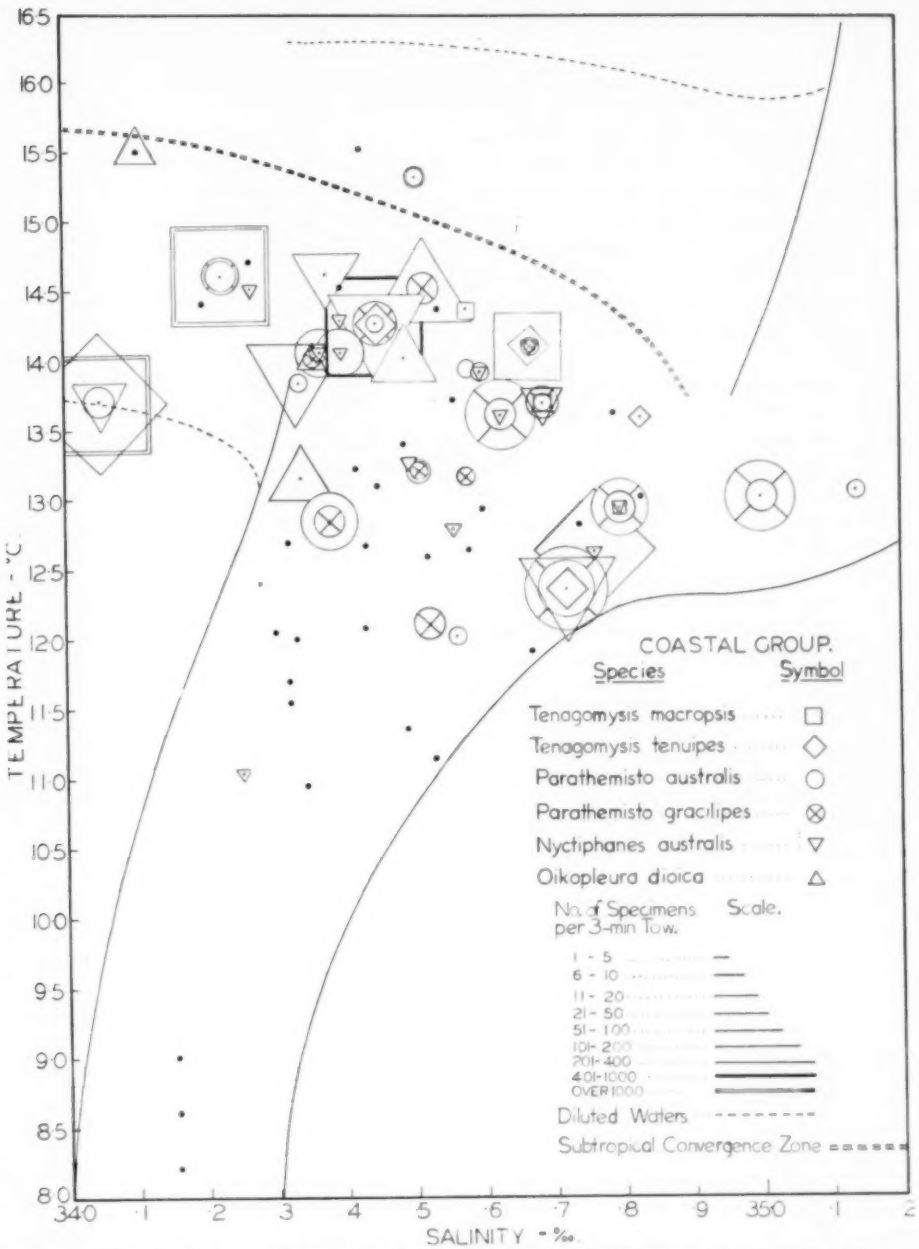


FIG. 9. The distribution of Coastal species in the T-S-P diagram. These species occur commonly over comparatively wide salinity and temperature ranges. They do not occur in subantarctic water except where it is intruding into, and mixing with, the coastal water. Plankton stations at which no specimens of the group were taken are shown by ●

aggregation (except Station 125), suggesting little or no influence from water of subtropical origin. A third group of stations yielded comparatively small mixed catches of Coastal, Subtropical, and "Tolerant" Southern Subantarctic species, which indicates that mixing was also taking place. This mixing may have been on a minor scale or the small catches may be due to the tows being made in daylight. The stations form a discontinuous series extending more or less vertically through the diagram to terminate at Stations 130 and 138.

The distributions of the groups in Figure 10 are brought about by movements of the waters of which they are indicators. Therefore, the general courses of such movements should be traceable from these distributions. The fact that subtropical oceanic species are present in the coastal water indicates that water of subtropical origin is moving into the coastal water. Similarly the distribution of the Subantarctic species shows they also are being carried into the coastal water. These movements are shown by stippled arrows in Figure 10. Those portions of the T–S–P diagram which are illustrative of intensive mixing of plankton and waters suggest that, as well as these general movements, there are others in which there is a more vigorous, localised penetration shorewards. It would seem that these are predominantly of water of subantarctic origin, intruding into coastal water.

A number of the stations of each of the regions of mixed waters in Figure 10 are widely distributed geographically and in time. Nevertheless, where similar environmental properties have ensued on the mixing of the waters, the group composition of the plankton hauls, and often the quantity collected, are comparable. Thus in this T–S–P diagram, the selected representatives of the zooplankton emphasise and enable the identification of those stations at which mixing of waters is inducing similarities in the environmental conditions. Conversely, the diagram shows for those stations at which one group of species is present, or predominates, that the water is entirely or predominantly of that mass for which the species constitute an indicator group.

It can be argued with respect to the "faunal island" about Stations 322 and 326 (Fig. 10) that more frequent sampling would have revealed a continuity in the species distribution between these and other stations of the series (Fig. 2). In all, seven salinity–temperature and plankton stations were occupied near to and north of what is believed to be the subtropical convergence (Figs. 4*a*, 19*b*), and all are located in the T–S diagram (Fig. 3) in water of subtropical origin.

Waters of mixed properties undoubtedly occur about the convergence. However, should water of either subtropical or subantarctic origin be present in slightly greater quantity, stations would tend to aggregate in the one or the other in the T–S diagram. The predominating water would be reflected in the species which were present. On the other hand, if samples are from truly intermediate conditions, an intermediate position would be occupied in the diagrams; but if the transition zone is narrow (as in the present traverse, see Fig. 4*a*), such samples would be rare. The subtropical group of species predominated at Stations 322 and 326, which agrees with the stations being north of the convergence and in water largely of subtropical origin (some Subantarctic species were taken, but they are believed to have originated in the subsurface subantarctic water, see p. 47). In the circumstances, therefore, it seems reasonable to separate Stations 322 and 326 from the remainder.

GEOGRAPHICAL DISTRIBUTIONS OF TEMPERATURES, SALINITIES, AND SELECTED SPECIES, AND CORRELATION OF THESE WITH THEIR DISTRIBUTIONS IN T–S–P DIAGRAMS

A sequence of geographical charts incorporating synoptic or quasi-synoptic collections of temperatures and salinities should demonstrate cyclical or other changes in the distri-

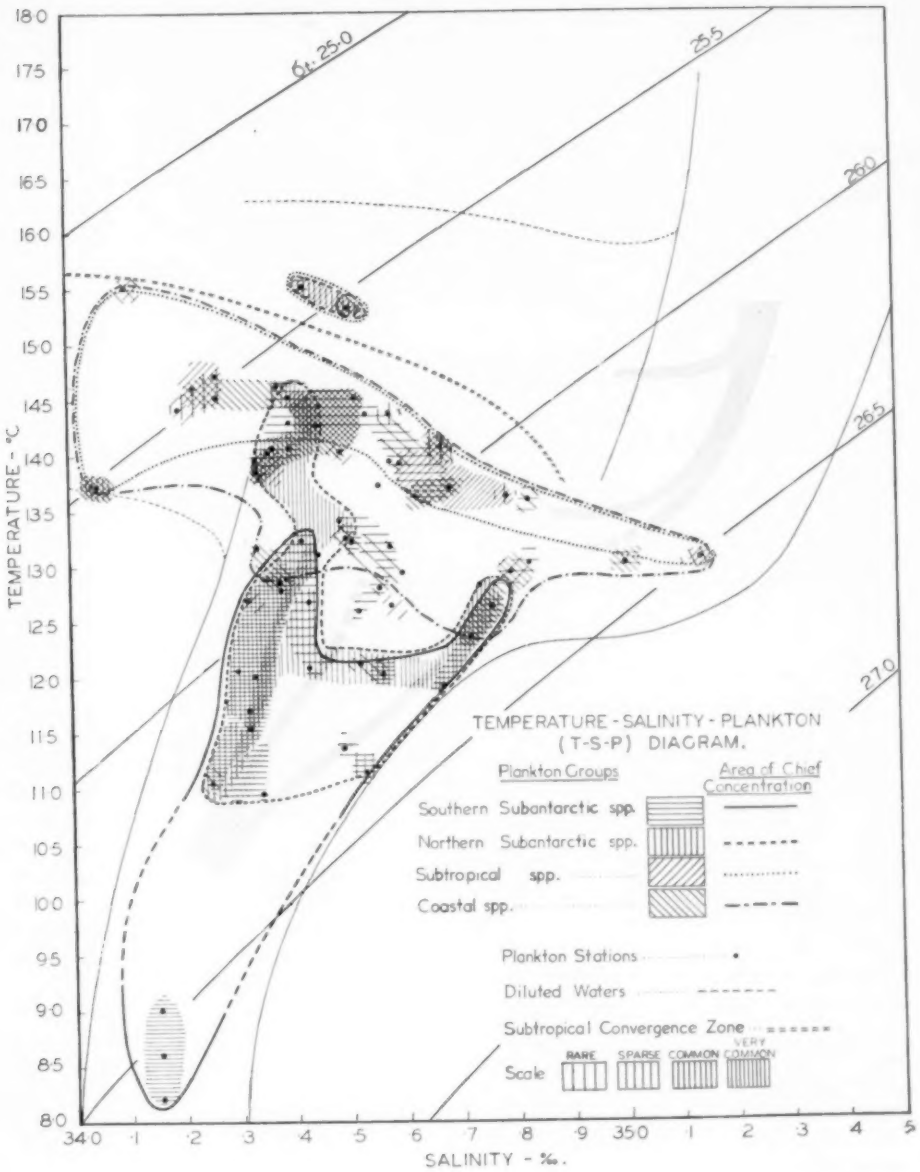
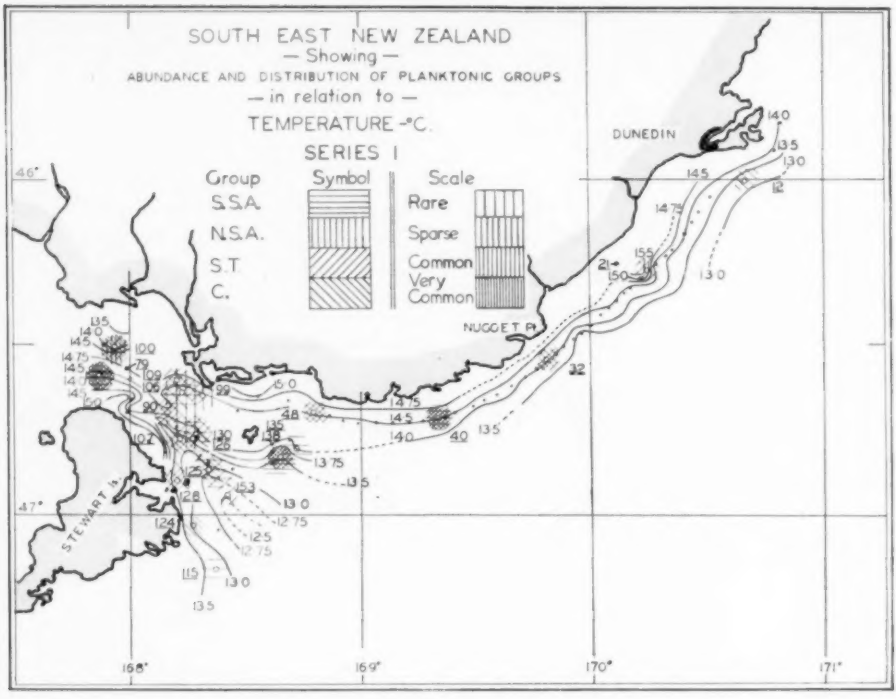


FIG. 10. A generalised T–S–P diagram in which the distributions and interrelationships of the four planktonic groups from the waters about southern New Zealand are shown. Note the three areas where mixed plankton catches indicate that mixing of waters is taking place. The water envelope is as in Figure 3; only plankton stations are entered.



FIGS. 11, 12. Series 1, Stations 10–153, January 6–24, 1951. The distribution of Southern and Northern Subantarctic, Subtropical, and Coastal species in relation to Figure 11, Temperature, °C.; and Figure 12, Salinity, °/₀₀. S.S.A. (Southern Subantarctic group); N.S.A. (Northern Subantarctic group); S.T. (Subtropical group); C. (Coastal group). Temperatures or salinities additional to those taken at plankton stations • ; plankton station numbers are underlined.

butions of the properties of an area. In turn such changes may be correlated with variations in the geographic distribution of the plankton to yield information showing the causes and effects of water movements on species distribution. Accordingly the geographical distributions of water properties and of plankton groups are discussed for the stations of Series 1 to 7. The relationships thus disclosed are considered with reference to the distributions in the T–S–P diagrams.

Series 1. Stations 10 to 153; 6 to 24.I.51

The stations of Series 1 were accumulated over a period of 18 days. Of these, Stations 10 to 48 were occupied during January 5 to 6, 1951. Charts of the distributions of temperatures and salinities (Figs. 11, 12) illustrate an average of conditions because of the length of time involved.

Warm, comparatively highly saline water extends from the western and central Straits along the South Island coast, and has probably originated in that Tasman Sea water which has been deflected to the southward along the west coast of South Island. It is being diluted by fresh water. Other highly saline water appears to be entering from Patterson Inlet, and spreads thence south-eastwards along the coast of the island. Cooler water (Fig. 11) is present as a tonguelike intrusion

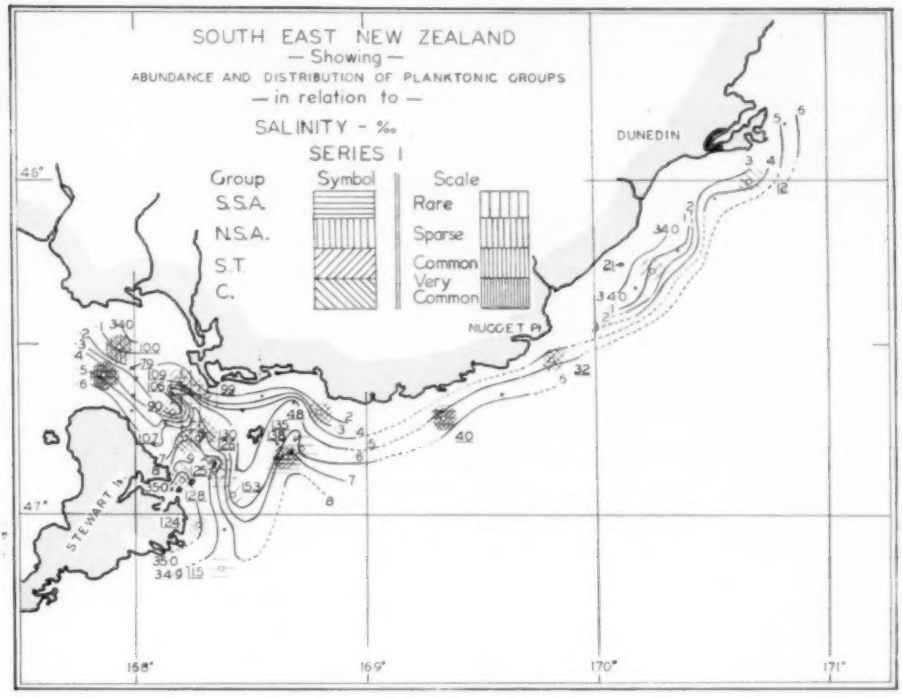


FIG. 12. See legend for Figure 11.

from the southeast. However, the distribution of salinities suggests that highly saline water has spread throughout the area.

Only some general features of the plankton distribution in relation to that of the water properties will be discussed. From the T–S diagram (Fig. 3) it is apparent that the stations of Series 1 lie predominantly in the warmest waters, only a few being slightly influenced by the cool water from the southeast—a condition conforming more to that indicated by the distribution of salinities (Fig. 12). However, the T–S–P diagrams (e.g., Figs. 6, 10) demonstrate that Subantarctic species were present, in small numbers, at several of the stations. Thus indications are that water of subantarctic origin is entering Foveaux Strait, some of it probably from the southeast, as is suggested by the conformation of the isotherms (Fig. 11).

Station 79, and the geographically close Station 100, both possess a strong representation of Subantarctic species. In the T–S–P diagram (Fig. 10) Station 79 forms one of that group of stations at which occurrences of all plankton groups are suggestive of a mixture of all waters. It is likely, therefore, that subantarctic water is present, entering probably from the west, along with mixed coastal–subtropical waters. That the influence of this subantarctic water is weak is suggested by both the positions of Stations 79 and 100 in the T–S diagram (Fig. 3), and the lack of any indication of the water about them in the relevant geographic charts (Figs. 11, 12). Station 138 is in that part of the T–S–P diagram (Fig. 10) representative of mixing on a minor scale, and Subantarctic, Coastal, and Subtropical species were collected. The configurations of the isolines indicate a small-

scale intrusion of water of subantarctic origin into coastal–subtropical waters at Station 138. Thus the planktonic occurrences accord with the influences bearing at that point.

Occurrences of zooplankton at other stations could be individually discussed, and rational explanations of the presence or absence of groups can be advanced for many of them, but the detailed picture that results is a confused one. The waters are very mixed. The distributions of the species' groups are to an extent reflecting this state, which is aggravated by the long period over which sampling continued.

It is reasonable to deduce, from the physical data presented in Figures 11 and 12, that there is some influence from water of subtropical origin in Foveaux Strait. The presence of typically Subtropical species is supporting evidence. More conclusive evidence for the influence is demonstrated, however, from the distributions of the Subtropical species in the T–S–P diagrams (Figs. 8, 10, in particular). The occurrences of these species coincide with the distribution of the warmest waters which are in such a position as to be contributed to directly from the subtropical mass (Figs. 3, 10). Subtropical species were collected also at stations in later series (Stations 178, 199, 239, 292, 304); these occurrences are indicative of coastwise extension of the subtropical influence.

Series 2, Stations 159 to 192; 29.I.51 to 1.II.51

The stations of Series 2 (excepting along the coast of South Island) are eastward of, and a little further to seaward than, those in Series 1 (Figs. 1, 13). Cooler temperatures than those in Series 1 prevail along the coast of South Island, and there is a broad intrusion of cool water (Fig. 13) from the south and east. There is, too, an admixture of high salinity water throughout the sampled area (Fig. 14). A northwest to southeast displacement of the isolines about Stations 189 and 190, eastward of Steward Island, suggests that warm, high salinity water is present, possibly from Foveaux Strait.

Very common occurrences of Northern and Southern Subantarctic groups of species at Stations 187, 188, 189, 190, and 192 are believed to be indicative of a strong influence from water of subantarctic origin (Figs. 7, 10). Common occurrences of Coastal species at Stations 189 and 190 point as well to mixing between the coastal and subantarctic waters about these stations, and also suggest that the high salinity water extending from Patterson Inlet does in fact originate there, and is not an intrusion from other oceanic sources. The occurrences of the planktonic groups in relation to the geographic distributions of water properties (Figs. 13, 14) provide a similar picture. Stations 189 and 190 lie on the southwest side of the intruding low-temperature water. Mixing is undoubtedly taking place about these stations between this and the warm, saline Straits water. The collections of mixed planktonic groups confirm this. Stations 187, 188, 191, and 192 are closely associated with the intruding cool water (Fig. 13), which the predominance of Subantarctic species indicates is of subantarctic origin.

Stations 178 and 165 lie in high salinity, warm inshore water (Figs. 13, 14), and the Coastal and Subtropical species at both stations are in agreement with this. In addition, mixing with subantarctic water is indicated for Station 178 by the Subantarctic species occurring there. The regularity of the isolines in the vicinity of the station denotes that the waters are mixed, which agrees with Station 178 being (together with Stations 138, 135, and 130, Series 1) in that portion of the T–S–P diagram (Fig. 10) representing mixing of waters on a minor scale.

Stations 187 to 192 are moderately separated geographically, but their grouping in the T–S–P diagram demonstrates a certain homogeneity of environmental conditions. The diagram heightens the effect that coastal water has on the composition of the plankton

at Stations 189 and 190, but at the same time demonstrates an overall influence from Subantarctic species which are being introduced by water of subantarctic origin.

Subantarctic species, and water of subantarctic origin, are more in evidence at stations of Series 2 than at those of Series 1 (for which Subtropical species indicate that at least some of the water has originated in the subtropical mass). The differences between the series are concisely illustrated by the T–S–P diagrams (Figs. 7, 8, 10).

Series 3. Stations 193 to 228; 5 to 13.II.51

The beginning of Series 3 is separated by four days from the end of Series 2. In Series 2, lower temperatures than in Series 1 pointed to an increased subantarctic influence off the coast of South Island. In Series 3, cool, low-salinity water has intruded strongly towards the coast, centred a little to the west of Stations 216 and 218 (Figs. 15, 16). This intrusion appears to be acting as a barrier to an east-going coastwise movement of warm, high-salinity water, causing it to spread in a fanlike manner towards the southeast. High salinities and temperatures to the east of Stewart Island suggest that some of this water may be escaping in a narrow zone along the coast of the island. The isohalines and, to a lesser extent, the isotherms indicate that the influence of the cool, low-salinity water extends well in towards the Strait.

Apart from an exceptional occurrence of a Coastal species at Station 212, the plankton taken at Stations 210, 212, 214, 216, 218, and 206 is entirely of Southern and Northern Subantarctic groups (Figs. 10, 5, 6, 7). The water at these stations, therefore, is regarded as being of subantarctic origin. The stations are moderately separated geographically (Figs. 1, 15). However, their aggregation in the T–S and T–S–P diagrams (Figs. 3, 10) emphasises an essential homogeneity of the water which the occurrences of the subantarctic species confirm.

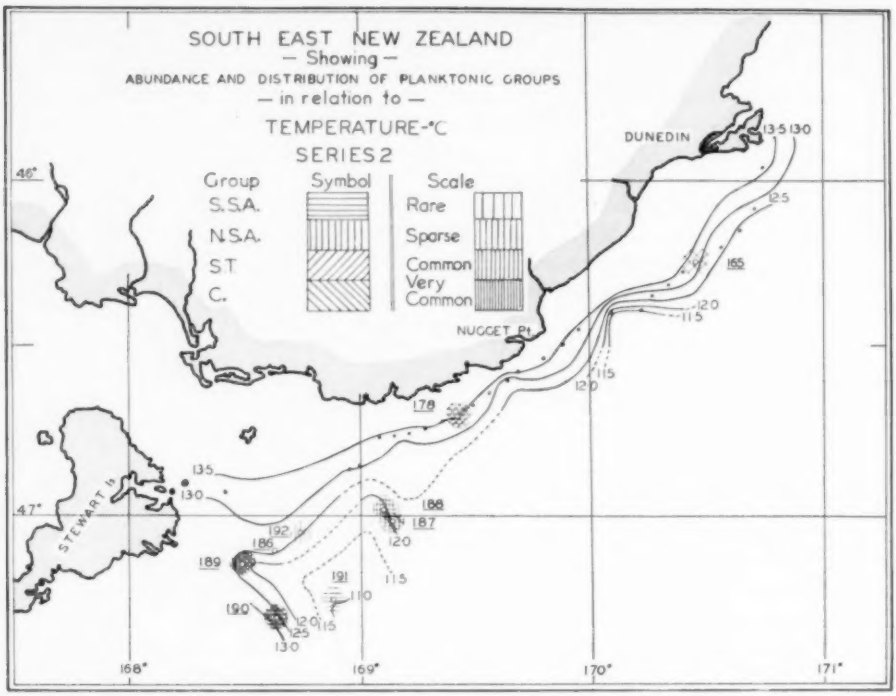
Four stations, namely 218, 208, 198, and 199 are located in water of slightly higher salinity (Fig. 10) than the other stations of the Series, possibly as the result of coastal water mixing with that from the subantarctic. Occurrences of Coastal plankton at 208 and 198 support this view; the subantarctic influence is evident from the Southern Subantarctic species captured at 218 and 198, and Northern and Southern Subantarctic species at 208. (No selected species were taken at Station 199.) From the geographic charts Station 218 appears from its temperature (Fig. 15) to be influenced by subantarctic water; on the other hand, the comparatively high salinity suggests some influence from coastal–subtropical water. As Southern Subantarctic species only were taken, the latter influence was not confirmed by the plankton haul. The temperature and salinity at Station 208 indicate that it is located in mixed waters and its plankton content supports this.

It is of interest that the distribution of the selected Subantarctic species of Series 3 indicates that uncontaminated water of subantarctic origin has a restricted salinity range of between about 34.2 and 34.45 °/₀₀ (Figs. 3, 10).

There are distinctive characteristics to the species composition of stations in this, as compared with the previous two series, which are readily seen from the T–S–P diagrams. They are believed to be directly attributable to the different properties which are evident between the waters of the three series. Unlike Series 1 and 2, water of subantarctic origin is dominant in Series 3, and the occurrences of the Subantarctic species coincide with and, in fact, delineate its extent in the diagrams (Figs. 5, 6, 7, 10).

Series 4. Stations 229 to 314; 8 to 9.III.51

The collections of this, and the subsequent, series are as nearly synoptic as is possible from a single ship. Stations of Series 4 were occupied approximately one month later than those of Series 3.



FIGS. 13, 14. Series 2, Stations 159–192, January 29–February 1, 1951. The distribution of the four planktonic groups in relation to Figure 13, Temperature, °C.; and Figure 14, Salinity, °/₀₀. S.S.A. (Southern Subantarctic group); N.S.A. (Northern Subantarctic group); S.T. (Subtropical group); C. (Coastal group). Temperatures or salinities additional to those taken at plankton stations ● ; plankton station numbers are underlined.

When compared with Series 3, higher temperatures near the coast of South Island (Fig. 17) point to a restoration of the influence of mixed coastal–subtropical waters, originating probably in the west. A slight influence from water of subantarctic origin is indicated by the shoreward deflections of isotherms south of Nugget Point. The pronounced shoreward bulges of isotherms and isohalines at a number of other localities are suggestive of stronger influences from the same source (Figs. 17, 18). The conformation of these isolines may suggest as well an offshore movement of coastal water in adjacent areas. Steep temperature gradients between the warm saline coastal and the cool, less saline oceanic waters are suggestive of mixing, over short distances. There is an area of more general mixing extending from shortly south, to north, of Dunedin.

In the T–S diagram (Fig. 3) the plankton stations of Series 4 lie in a group between 11.75° and 14.5°C., and (all but Station 239), between 34.3 and 34.4 °/₀₀ salinity. Thus they are closely associated with Stations 212, 214, etc., of Series 3. At each of Stations 270, 285, 297, 301, and 308 there is a strong representation of Northern and Southern Subantarctic planktonic groups (Fig. 10). Therefore, the position of the stations in the T–S diagram, and their plankton content, associate them with the water of subantarctic origin. The

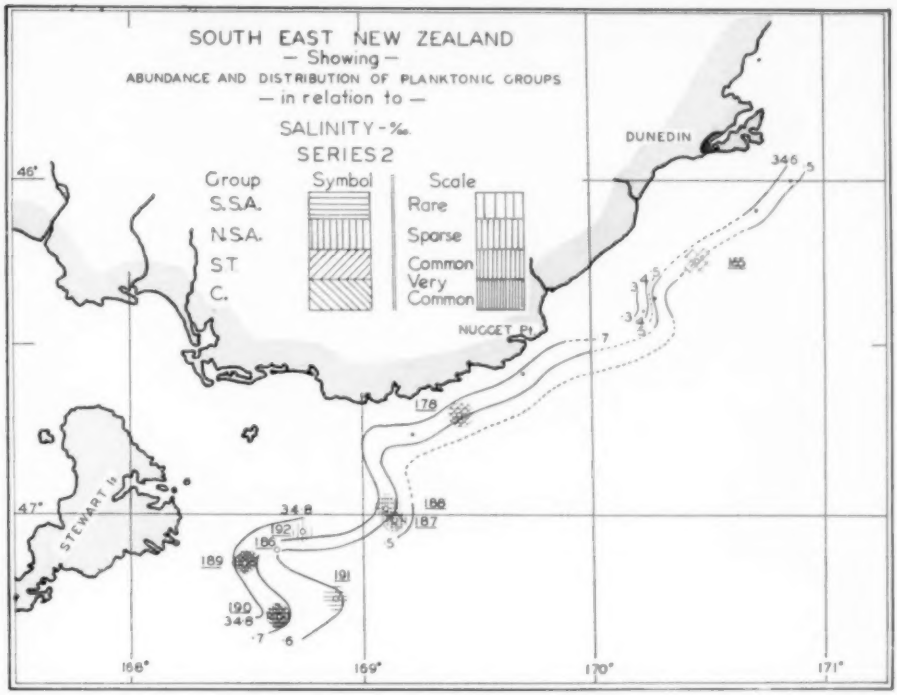


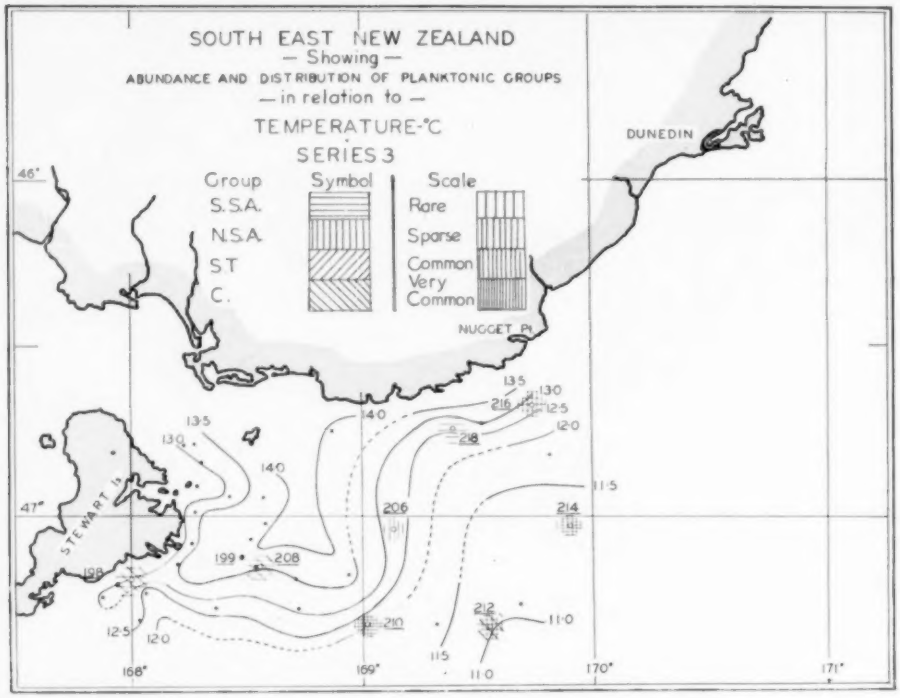
FIG. 14. See legend for Figure 13.

subantarctic influence is confirmed by the geographical distribution of temperatures at Stations 285 and 297 (Fig. 17), and salinities at 270, 301, and 308 (Fig. 18).

Of the remaining stations in Series 4 (Stations 292, 310, 279, 244, 304, and 239), Station 239 lies in coastal water (Fig. 10), but exceptionally contained a rare representation of the Southern Subantarctic Group; this group was present also at Station 244. Temperatures indicate that subantarctic water may be influencing these two stations (Fig. 17) which possibly explains the plankton occurrences. Nevertheless Coastal and Subtropical planktonic groups would have been more appropriate, especially at Station 239.

Stations 292, 310, 279, 304, and 244 are grouped together in the T–S–P diagram and the mixed Coastal, Subtropical, and Subantarctic (mostly Northern) plankton at most of them denotes they are sampling in a mixture of subantarctic and coastal–subtropical waters. Isotherm configuration (Fig. 17) indicates that, following an initial mixing between water of subantarctic origin (as is present at Stations 285, 297, and 308) and coastal water, the influence of the subantarctic water continues shorewards towards Stations 279, 292, and, to a lesser degree, 310. Isohalines (Fig. 18) point to Station 304 being influenced by water of subantarctic origin as well.

Series 4 is important for two reasons. First, Stations 292, 310, 279, 304, and 244 form a compact group in the T–S–P diagram (Fig. 10). These are geographically isolated sta-



FIGS. 15, 16. Series 3, Stations 193–228, February 5–13, 1951. The distribution of the four planktonic groups in relation to Figure 15, Temperature, °C.; and Figure 16, Salinity, °/₀₀. S.S.A. (Southern Subantarctic group); N.S.A. (Northern Subantarctic group); S.T. (Subtropical group); C. (Coastal group). Temperature, salinity additional to those taken at plankton stations ● ; plankton station numbers are underlined.

tions, but they are aggregated because of similarities of hydrological and biological properties, which are the result of invasions into coastal water, at several localities, of water of subantarctic origin. Second, coastal and subantarctic waters in the T–S and T–S–P diagrams are linked through a continuous series of stations. Such a linkage demonstrates beyond reasonable doubt that the Subantarctic plankton collected in the coastal area originates, and is transported, in water of subantarctic origin which is penetrating shorewards (and at the same time is being warmed). These two facts thus contribute evidence in support of an earlier statement that planktonic content of mixing waters may be utilised to indicate the sources of the waters being mixed.

The T–S–P diagram (Fig. 10) emphasises the similarities in planktonic content and hydrologic conditions between Series 3 and 4, even though they are separated geographically by at least 60 miles, and by almost a month in time. Of interest also, is that while subantarctic groups penetrated into warmer waters at Stations 279, 292, 304, and 310, coastal species did not penetrate to Stations 285 and 297, lying predominantly in subantarctic water. Coastal and Subtropical species rarely were taken in subantarctic water, even when, as at these stations, the collections were made at the extremities of what may be regarded as offshore directed movements of coastal water.

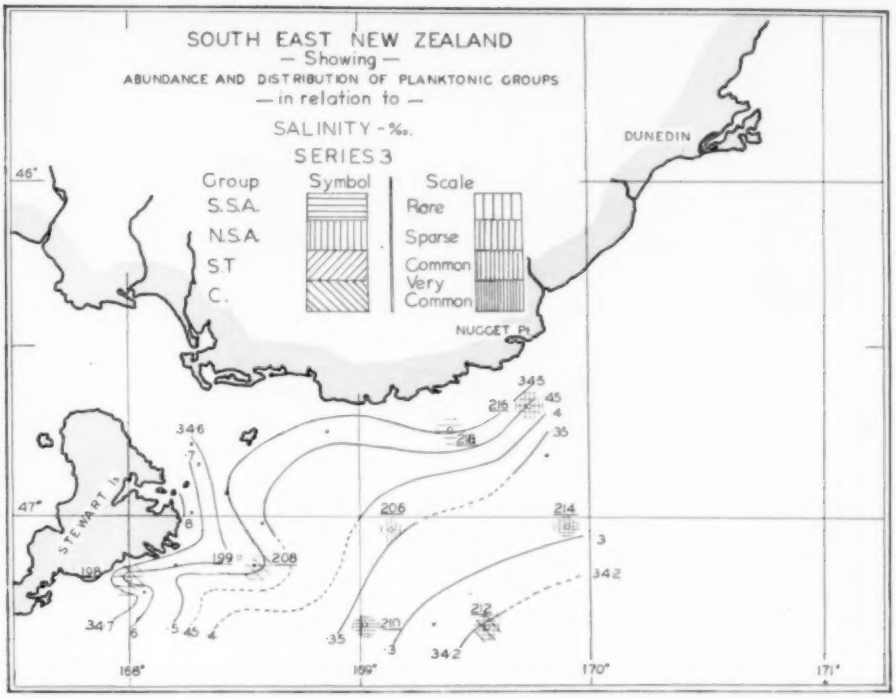


FIG. 16. See legend for Figure 15.

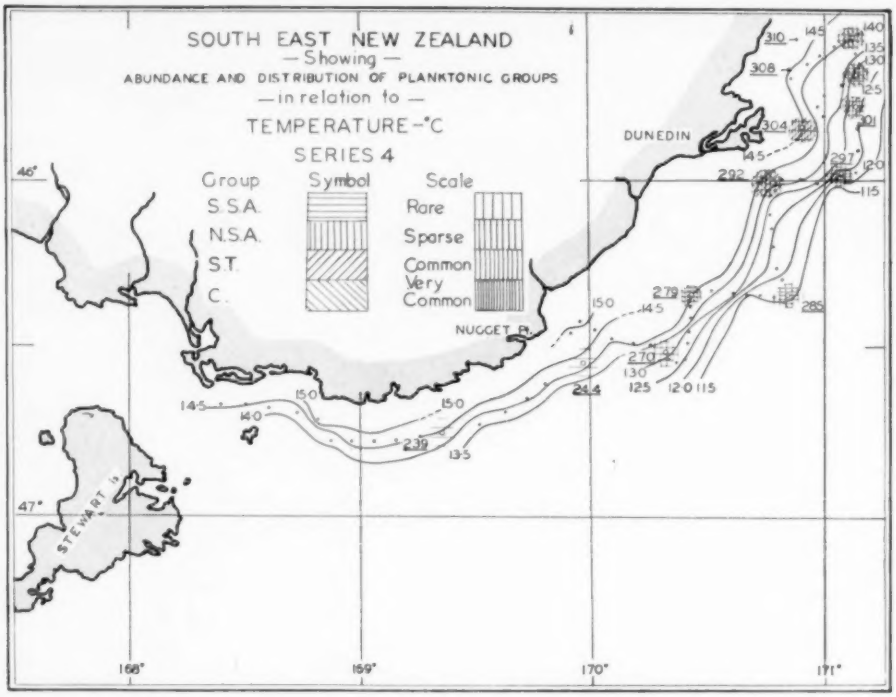
Series 5. Stations 1 to 6; 3 to 4.I.51

Stations of Series 5 and 6 were occupied during cruises between Wellington and Dunedin in January and March, respectively. Stations of Series 5 precede those of Series 1 by three days, but their discussion has been deferred for convenience of comparison with those of Series 6.

The stations of Series 5 are believed to sample either from water of subantarctic origin, or from a mixture of this and high-salinity, but *cool*, coastal water. The temperature and salinity at Station 5 (Figs. 19*a*, 20*a*) indicate the presence of water of subantarctic origin only. At Station 6 this water is predominant, but the slightly increased salinity points also to coastal water being incorporated. Higher salinities again at Stations 1 to 4, indicate an increased admixture of the coastal water. The steady rise in temperature northwards along the coast probably reflects a latitudinal increase. However, the distributions of temperatures and salinities demonstrate that the water is essentially homogeneous and predominantly of subantarctic origin. Supporting evidence comes from the planktonic occurrences.

Either or both Northern and Southern Subantarctic groups occur at Stations 2 to 6 (none of the species captured at Station 1 was among those selected). Coastal species were present at Stations 4 and 3, but they do not occur elsewhere. These distributions indicate the influence of subantarctic water at all stations, together with that of coastal water at Stations 3 and 4.

In the T–S diagram (Fig. 3) Stations 5, 1,



FIGS. 17, 18. Series 4, Stations 229–314, March 8–9, 1951. The distribution of the four planktonic groups in relation to Figure 17, Temperature, °C.; Figure 18, Salinity, °/₀₀. S.S.A. (Southern Subantarctic group); N.S.A. (Northern Subantarctic group); S.T. (Subtropical group); C. (Coastal group). Temperature or salinities additional to those taken at plankton stations • ; plankton station numbers are underlined.

and 2 lie within the narrow salinity range which appears to typify water of subantarctic origin. That only Subantarctic species occur at Stations 5 and 2 confirms this (Fig. 10). Stations 6, 3, and 4 occur over much the same temperature range, but at higher salinities. The occurrences of Subantarctic species testify to the influence of subantarctic water at these stations.

Although there are Coastal species at Stations 3 and 4, neither T–S nor T–S–P diagrams demonstrate a source for the water which transports the species. Nor do these diagrams show whence comes the more saline, cool water responsible for separating Stations 3, 4, and 6 from Stations 1, 2, and 5. The geographical distributions of salinities, temperatures, and plankton (Figs. 19*a*, 20*a*) demonstrate the probability that this water is coastal in origin. Seasonal temperature changes take effect more slowly in water than in air, and air temperatures, at the time of sampling, had not reached summer maximum. Therefore it is reasonable to expect comparatively cool coastal waters. The separation of the two lots of stations arises when this high-salinity, but cool, inshore water mixes with, but does not warm, the more offshore subantarctic water. In Series 6, on the other hand, the coastal water has a much higher temperature (Figs. 4*a*, 19*b*) and therefore raises the temperature of the subantarctic water with which it mixes;

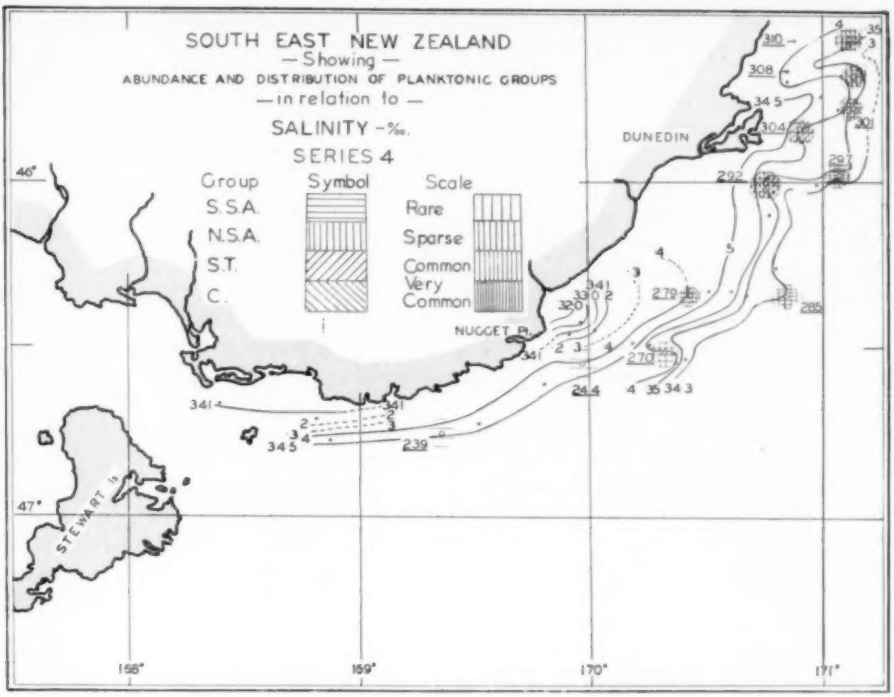


FIG. 18. See legend for Figure 17.

and, incidentally, makes for readier identification (in the T–S–P diagram) of the mixed sample.

Series 6. Stations 320 to 343; 21 to 22.III.51

These stations were occupied in March, and the shoreward extremity of the subtropical convergence now transects the series (see p. 22). Stations 320 to 328 are north of the convergence, 331 to 343 to the south of it; Stations 329 and 330 are near to the meeting zone of the subtropical and subantarctic waters (Figs. 4*a*, 19*b*, 20*b*).

Subantarctic water is strongly evident, through low temperatures and salinities, only at Stations 341 to 343. Northwards towards the convergence there is a pronounced coastal influence shown by high temperatures and also by increased salinities (salinities decrease farther inshore as a result of dilution with fresh water). North of the convergence, the salinities at some stations approach those of open ocean subtropical water (about 35 ‰), but dilution is apparent and to a considerable degree at Stations 322 and 326.

Southern and Northern Subantarctic species occurred at Station 326, and Northern species at 322. They are probably to be accounted for by upward migration of the organisms from the subsurface subantarctic water.

The occurrences otherwise of the several planktonic groups conform to the distribution of the waters. Station 342 has only Subantarctic groups present, but at Station 337 these groups are rare and the Coastal Group predominates. At Station 330 there is a mix-

ture of the four groups, but at 326 and 322 the Subtropical Group is dominant.

The T–S–P diagram (Fig. 10) illustrates the general correlation between the occurrences of planktonic groups and the distribution of the water properties shown in the geographical charts. Station 342 is the only one clearly in subantarctic water and its fauna is entirely of Subantarctic groups. Station 330 is situated in the portion of the T–S–P diagram representative of water of subantarctic origin intruding into, and mixing with, coastal–subtropical waters. The four planktonic groups are present, which is consistent. However, both its position in the T–S–P diagram, and the predominance of Subantarctic species indicate that the subantarctic influence is strongest. Station 337 lies just outside the larger of the subantarctic intrusions in the T–S–P diagram. Isotherms and isohalines (Figs. 19*b*, 20*b*) suggest a strong coastal influence, which is confirmed by the predominance of Coastal species. Stations 326 and 322 are separated from all other plankton stations by the subtropical convergence. Both occur in water of subtropical origin, somewhat diluted by lower salinity coastal water, and Subtropical species predominated in the plankton.

It is important that the species' occurrences of Series 6 indicate the approximate position of the subtropical convergence. A comparison of faunal distributions, as well as physical data, of Series 5 and 6 show that the convergence has moved southwards during the three months separating the series.

Series 7. Stations 795 to 921; 13 to 17.XI.51

The stations of this series have enabled the source of the Southern Subantarctic species to be demonstrated, and have distinguished them through their origin in cold water from the Northern Subantarctic group. The temperatures and salinities of the stations are within those given for subantarctic water by Deacon (1937). Because water samples were lost, the salinities of the three plankton stations 795, 826, and 921 have been arbitrarily chosen from within the range indicated by other stations in the series. The north-going component in the West Wind Drift, ensures that the influence of water in the latitudes of Stations 826 and 921 eventually will be felt about southern New Zealand. Through its agency, the more adaptable of Southern Subantarctic species will be transported to the nearshore waters. The temperature at Station 795 was 2°C. lower than any from which the Northern Subantarctic Group was taken. It would appear that this difference may be adequate as a barrier to these species in view of the geographical proximity of the station to Foveaux Strait (Fig. 2).

DISCUSSION

The selection of those species which are most representative of the faunas of particular waters can be made from the species' distributions in relation to temperature and salinity with the aid of the T–S–P diagrams. In turn, the extent of the influence of water bodies entering an area can be assessed through the distribution of the species in the T–S–P diagram, as well as by the temperatures and salinities of the waters. Species selected as representative of the fauna of one water may occur in other waters, often at groups of stations for which there are similar properties of temperature and salinity. The stations of such a group may be widely scattered in time and place, but affinity between them is demonstrable by means of their species' content. Thus the species relate the waters at the stations to their sources, and at the same time demonstrate the direction and extent of the water movements which have brought about the planktonic distribution. Because the species of a group indicate the presence (and source) of a water body, therefore the distribution of this water in another with which it is mixing can be traced in the T–S–P diagram through the distribution of these species.

The study raises problems relating to the transfer of organisms between one body of water (or range of conditions) and another.

Physiological adaptability probably plays a major part in deciding whether a species will survive such a transfer. For example, "Intolerant" species, because they were apparently unable to adapt readily, show sharp reductions in numbers as coastal water is reached, while the more adaptable "Tolerant" species penetrated into it more freely (Figs.

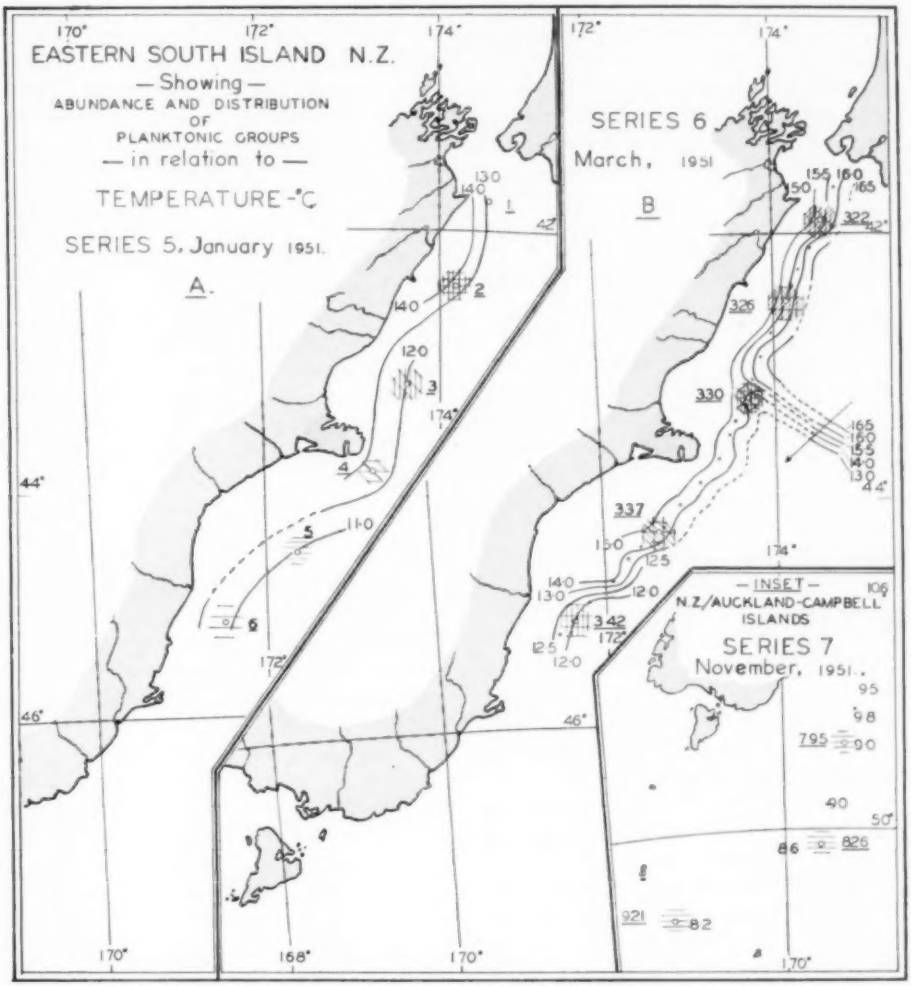


FIG. 19A, B. The distribution of the four planktonic groups in relation to temperature for A. January 1951; Stations 1–6. B. March 1951; Stations 320–343.

INSET: November 1951; Stations 795–921.

The break in temperatures across the subtropical convergence in B are drawn in conjunction with data from the surface thermograph trace, Figure 4*b*. The symbols for the planktonic groups, and the scale of abundance, are as in Figures 10–21.

5, 6). On the other hand, it has been remarked that Coastal species have not penetrated into water of subantarctic origin. A possible explanation of these facts is that some cold-adapted Subantarctic species can survive the increase in temperatures between cold subantarctic and warm coastal waters, but that coastal species are unable to adapt to lower temperatures. It is difficult to see that this explanation is totally adequate. A preponderant one-way movement of Subantarctic species into coastal areas is demonstrated in the T–S–P diagram (Fig. 10), and is also apparent from analysis of the plankton catches at stations of Series 4 for example (Figs. 17, 18). When oceanic waters move into coastal water, compensatory movements out of the area should ensue. At least some of the low-density inshore water might escape by overriding denser subantarctic water, in which case coastal species would be carried offshore and their numbers gradually decrease as environmental conditions become adversely modified. The opposite appears to be true in most instances. The numbers of the Coastal group of species captured decrease abruptly between 12.5 and 13.0°C. (Fig. 9), as the oceanic water is reached, e.g., as at Stations 285, 297, Series 4. It seems unreasonable to suppose that the abruptly effected absence of the Coastal species results from a sudden application of some physiological factor, and it is suggested that there may be reasons involving hydrological phenomena.

It is possible that the northeast moving current along the coast sets up a superficial transverse circulation (Sverdrup *et al.*, 1942: 676–677) which passes surface oceanic water shorewards. It is conceivable that offshore, surface transport of organisms could be prevented by the development of such a circulation. This mechanism would tend to accumulate less dense water to the left of the direction of flow, i.e., along the coast. In turn, this would facilitate a lateral, offshore transfer of water, and the contained organisms, at deeper horizons. However, such would not be revealed by the surface sampling of this survey.

A second possibility is that the transfer between the coastal and subantarctic waters proceeds through the agency of discrete pockets of water, formed on a small scale but in an analogous manner, to those between the Gulf Stream and neighboring waters (Iselin and Fuglister, 1948; Ford and Miller, 1952). Isoline configurations in several of the Figures 11–20 suggest the development of pockets on the shoreward side of the northgoing oceanic waters. If the transfer of surface water were largely shorewards, as seems possible, it would assist in explaining the abrupt cessation of the offshore occurrences of Coastal species.

The method of the T–S–P diagram is suitable for determining the tolerances of species to temperature and salinity in that it demonstrates their reactions to changes in environmental conditions. The fact that data are collected in the field is advantageous and especially so when considered in conjunction with experimental evidence, for example of the long or short term temperature adaptability of species. Sheard (1953: 21, and personal communication) indicates that temperature tolerances may vary according to the range to which the local stock of a species has become adapted; the occurrences of *Thysanoessa gregaria* in the present survey appear to be a case in point. In general, *Th. gregaria* is rarely captured in subantarctic waters (Sheard, 1953; Boden, 1954). But it was consistently taken as a Southern Subantarctic species during the present survey. It reacted to increasing temperatures (Fig. 6) by a reduction in numbers in a manner similar to other species of the Southern Subantarctic Group. It is possible that this may be a stock of *Th. gregaria* which is adapted to cold water. If so, considerable interest would accrue at this stage in comparing upper and lower temperature tolerances of this and Subtropical stocks, both by experiments and through field data by means of the T–S–P diagram.

The technique of the T–S–P diagram has

been confined to surface waters in this study. It is applicable, however, to determining relationships between plankton and water masses in a vertical direction. David (1955), and others, have been concerned with the vertical distribution of species on an ocean-wide scale, but the method equally applies to much more limited areas. It should prove of value also in studies of plankton–water relationships near convergences, areas of up-

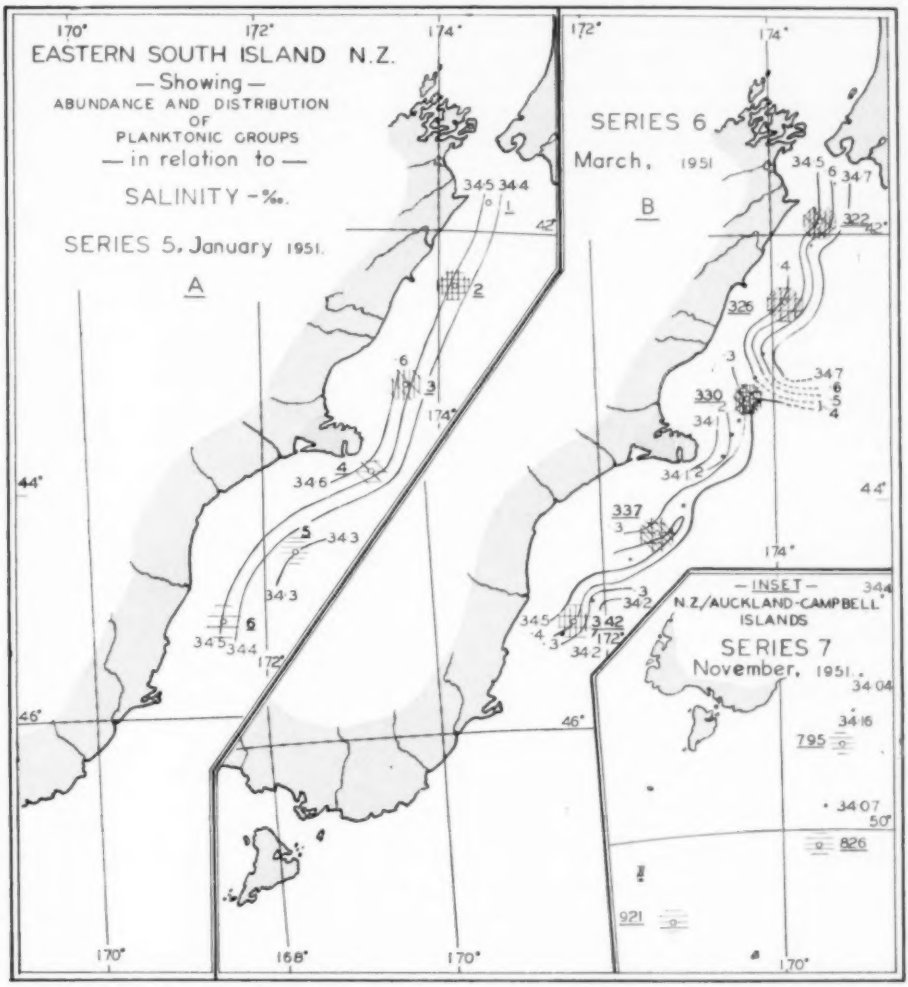


FIG. 20A, B. The distribution of the four planktonic groups in relation to salinity for A. January 1951: Stations 1–6. B. March 1951; Stations 320–343.
INSET: November 1951; Stations 795–921.

The position of the subtropical convergence in B is suggested by the dashed isohalines near Station 330. The symbols for the planktonic groups, and the scale of abundance, are as in Figures 10–21.

welling, in water masses surrounding small islands, and it may be of considerable value in the study of patchiness in the distribution of organisms, e.g., of aggregation in the statistical sense. There is little doubt that a comparable technique may be used to determine the effects on organisms of other pairs of environmental factors and in this connection the use by Moore (1950, 1952) and Moore, Owre, Jones, and Dow (1953) of the light and temperature relationships of euphausiids and other zooplankton should not be overlooked. Last, a convenient, three-dimensional picture of the distribution of a species would be presented if a T–S–P diagram, constructed from data from vertical series of samples, were allied with the geographical distribution of the species.

SUMMARY

1. Two principles concerning plankton distribution have been established by earlier workers. First, bodies of water with distinct properties possess distinctive planktonic faunas. Second, when one of these bodies of water mixes with another, the faunas are mixed. In this present study, species have been selected as indicators of the constituent waters of an area about southern New Zealand where waters of subtropical and subantarctic origins are mixing together, and with coastal water. The surface waters entering the area are identified by their temperature–salinity relationships.

2. All occurrences of a number of selected species of the plankton have been superimposed on the T–S diagram of surface waters in the area to produce the temperature–salinity–plankton (T–S–P) diagram. It is found that the distribution of each of the several waters coincides with the distribution of its indigenous species. Further, where one of the waters penetrates into, and mixes with another, it is demonstrated that the species of the one are transported into the other and a mixed fauna results.

3. Examples are discussed in which stations (isolated geographically and in time) aggregate in the T–S diagram. The similar environmental conditions which exist at these stations are the result of several intrusions at different localities of subantarctic into coastal water. The individual intrusions have been demonstrated by considering the geographic distribution of water properties in near-synoptic series of stations. The close affinity between the stations of each aggregate is demonstrated in the T–S–P diagram by means of the similarity of the plankton captured at the stations.

4. Plankton distribution in the T–S–P diagram, allied with that shown by the geographical distribution of the species, has demonstrated a southward migration of the subtropical convergence during the summer.

5. Temperature and salinity tolerances of species and the reactions of species, or groups of species, to changes in temperature and salinity, are readily observable in the T–S–P diagram.

6. The T–S–P diagram is potentially useful in studies of distribution about convergences, small islands, near areas of upwelling, and for studying patchiness of plankton.

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The Structure and Reproduction of *Gulsonia annulata* Harvey (Rhodophyta)

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Gulsonia HARVEY is a little-known monotypic genus of red algae which has been variously placed in the Cryptonemiaceae (Harvey, 1855, 1860), close to *Crouania* (J. G. Agardh, 1876; Schmitz, 1889) and to *Wrangelia* (J. G. Agardh, 1894, 1897), and in the Nemalionales near *Batrachospermum* (Schmitz and Hauptfleisch, 1897; Fritsch, 1945).

Gulsonia annulata was originally described by Harvey (1855) from Phillip Island, Western Port, Victoria and later (Harvey, 1860) recorded from Georgetown, Tasmania. Harvey's collections were apparently sterile, but later J. G. Agardh (1894, 1897), and Schmitz and Hauptfleisch (1897) described carpospores, tetraspores, and monospores without indicating the source of their material. Only in recent years has the alga again been recorded (Womersley, 1948, 1950).

During February, 1956, abundant drift material was collected at Pennington Bay, Kangaroo Island, by the authors. Some 90 specimens were collected as they were washed in over the reef, comprising 51 tetrasporic, 24 female and cystocarpic, 3 male, and 12 sterile plants.

Gulsonia annulata is also known from Sturt Bay on Yorke Peninsula and from Eucla, near the South Australian—Western Australian border. Apparently it is comparatively rare, only being found in drift material from well below low tide level; the plants decompose fairly rapidly when cast ashore.

The following account is based on the rich Kangaroo Island collection of February, 1956.

Shortly before this paper was submitted for publication, Kylin's (1956) account of the Rhodophyta became available. Here Kylin also recognises the identity of *Gulsonia* Harvey and *Crouaniopsis* J. and G. Feldmann, and transfers *C. annulata* (Berthold) J. and G. Feldmann to *Gulsonia* as *G. mediterranea* Kylin nom. nov. The same epithet had also been adopted for the Mediterranean species by the present authors. Kylin, however, gives little more than a formal generic description of *Gulsonia*, and his comments are apparently entirely based on the Mediterranean species.

VEGETATIVE FEATURES

The plants ranged up to 30 cm. in height with an average of 18 cm., and a main axis diameter of 2 mm. The thallus axis and branches are terete, uniaxial, and articulate, with each axial cell bearing from its upper end a whorl of four short branches of limited growth. These whorled lateral branches form nodal bands, less distinct in the youngest parts, where they almost completely cover the axis, and most prominent over the rest of the plant, except in the oldest parts of the main axis and branches where they become obscured (Fig. 1). This is due to the development of 1–3 descending corticating filaments from the basal cell of each short branch, which cover the axis and in the oldest parts of the plant form a dense, tough, and feltlike covering over the whorled laterals as well as the axis. The corticating filaments are simple or sparingly branched, of 7–10 elongate cells averaging 250–300 μ long, by 25–30 μ broad. The axial cells of the thallus are approximately twice as long as wide, reaching dimensions of 1300 μ by 700 μ at the base of the plant. The intercellular connection between cells shows a prominent, thickened platelike structure (Fig. 2c, d).

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FIG. 1. *Gulsonia annulata* Harvey. Habit of plant showing nodal formation except at base and tips of branches.

The lateral whorled branches consist of 5–7 orders of cells. Cells of the second order are formed dichotomously on the basal cell, thence each cell of successive orders produces a whorl of three cells except the outermost which are borne either in two's or three's. Occasionally the normal terminal cells are transversely divided (Fig. 2b). Cells of each order are progressively smaller, the terminal ones averaging 20 μ long by 6 μ broad. Hairs about 300 μ long, with a swollen tip, are frequently formed from the terminal cells (Fig. 2b). Reproductive organs, young vegetative branches and gland cells are borne on the lateral branch whorls.

Branching of the thallus is irregular, and young vegetative branches may occur on any, except the oldest, parts of the plant. Each

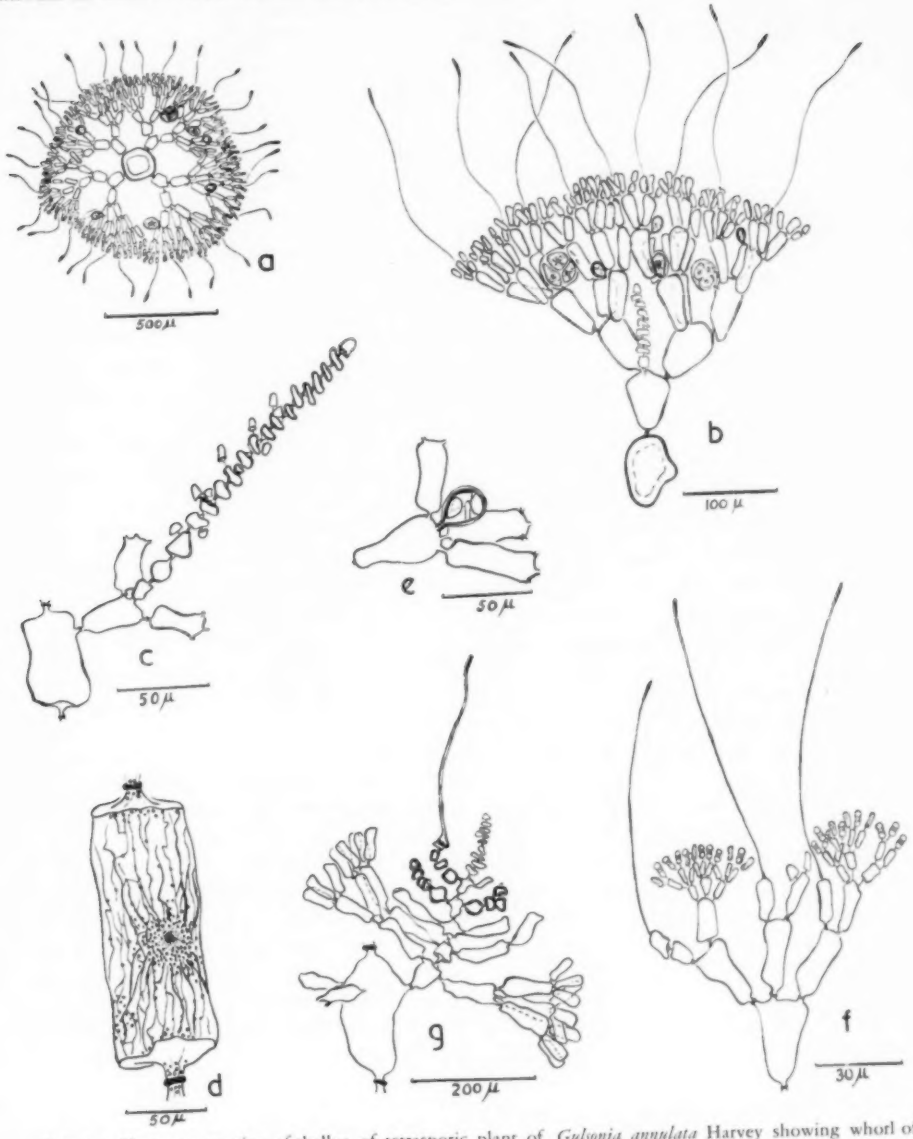


FIG. 2. a, Transverse section of thallus of tetrasporic plant of *Gulsonia annulata* Harvey showing whorl of four lateral short branches arising from axial cell; b, short lateral branch of *Gulsonia annulata* Harvey showing branching by two from basal cell and by three from each subsequent cell, young lateral branch, stages in development of tetraspores, scattered "gland" cells and terminal hairs from some cells; c, development of first lateral cells in young vegetative branch of *Gulsonia annulata* Harvey; d, mature axial cell of *Gulsonia annulata* Harvey showing chromatophore pattern, nucleus, and small granular inclusions; e, "gland" cell of *Gulsonia annulata* Harvey with inclusions; f, terminal spermatangia of *Gulsonia annulata* Harvey with median nucleus; g, fertile branch of *Gulsonia annulata* Harvey borne on basal cell of short lateral branch and bearing two carpogonial branches on the third axial cell and one on the fourth.

branch develops from the outer end of the basal cell of a lateral whorl member (Fig. 2b, c). The initial of the new branch divides transversely, forming a chain of 16–20 cells before cells in the central part of this chain divide laterally to cut off basal cells of the new whorl (Fig. 2c). These basal cells are arranged roughly in an anticlinal spiral, and divide rapidly to form the whorled laterals when the new branch emerges from within the old branch.

All cells are uninucleate, with a large, dense nucleus usually in the mid-part of the cell near the periphery. The chromatophores vary greatly in form, but are constant in any one type of cell. In the outer cells of the whorled laterals they are irregularly platelike, covering almost the whole periphery of the cell. As the cells increase in size the chromatophores change through an irregular anastomosing stage to branched, linear shapes in the larger cells of the main axes. These linear chromatophores tend to converge towards the nucleus (Fig. 2d). Carpospores and tetraspores contain chromatophores which form an irregular, granular network. The nodal or banded appearance of the thallus is accentuated by the denser chromatophores in the small outer cells of the whorled laterals, giving a deeper colour to the nodal bands. In older axial cells, covered by corticating filaments, the chromatophores are greatly reduced. Most cells contain numerous cytoplasmic granules, often concentrated around the nucleus, and at the cell junctions (Fig. 2d).

Pyriform "gland" cells, with a thick mucilaginous wall, occur on cells of the whorled laterals (Fig. 2b, e) in all plants. These cells average about 30 μ in length and each contains several larger inclusions of varying but definite form (Fig. 2e). These may be the "monospores" referred to by Schmitz and Hauptfleisch (1897), but are probably comparable to the gland cells of other genera of Ceramiaceae.

The whole thallus is enveloped in a mucilaginous matrix, making it quite slimy.

TETRASPORANGIA

Tetrasporangia are produced in the upper parts of the thallus, on the outer end of cells of the third order of the whorled laterals. Only one tetrasporangium develops on a single cell (Fig. 2a, b). The sporangium is at first spherical, uninucleate, and sessile, attached by a thin cytoplasmic connection. It reaches 70–80 μ in diameter before division commences. The nucleus divides twice, and with four nuclei present the protoplast division commences at the periphery and proceeds inwards, giving four uninucleate tetrahedrally arranged spores (Fig. 2b). Meiotic figures were not seen in the material available. Accumulation of Floridean starch is indicated by red staining with iodine in tetrasporangia over about 50 μ in diameter, the staining becoming deeper in mature spores. Mature tetrasporangia are about 80–90 μ in diameter.

SPERMATANGIA

Male plants bearing spermatangia are not easily distinguished from sterile plants, but are slightly paler in colour and "rougher" in appearance. This is due to the spermatangia which are formed from the majority of the terminal cells of the whorled laterals. Each normal terminal cell bears a further two or three whorls of small cells, the outermost being the spermatangia. These spermatangia are 8–9 μ long, constricted in the centre, with a median nucleus and two prominent vacuoles (Fig. 2f). Spermatangia are not formed from the occasional terminal cells which divide transversely. Spermatangia are 3.5–4 μ in diameter.

FEMALE PLANT AND CARPOSPOROPHYTE

In female plants, special branches, initially similar to young vegetative branches, occur at short intervals along the axis of main branches. However, normal vegetative growth ceases with the development of carpogonial branches, which are produced either singly or in opposite pairs. Most commonly the third

or fourth axial cell (from the base) of the fertile branch bears two carpogonial branches, while the cell above it (fourth or fifth) bears one (Fig. 2g). Carpogonial branches have, however, been found on axial cells up to the seventh, and occasionally four or five on one fertile branch. Only one carpogonial branch on each fertile branch ultimately gives rise to a mature carposporophyte; in fact, not more than one mature carpogonial branch with a trichogyne was ever observed on a single fertile branch.

An axial cell cuts off laterally a supporting cell of similar size (though later the axial cell is usually larger), which in turn gives rise to the first three cells of the carpogonial branch. At this stage the supporting cell and carpogonial branch are together about 50 μ long. The third cell of the carpogonial branch cuts off a fourth, the carpogonium which develops the elongate trichogyne (Fig. 3a, b). The trichogyne projects through the whorled laterals of the thallus, reaching a length of up to 350 μ (Fig. 3c).

Several spermatia may adhere to one trichogyne, but only one develops a connection through the trichogyne wall. Very soon after fertilisation the trichogyne disintegrates, leaving the four-celled carpogonial branch.

On the upper side of the supporting cell a rounded auxiliary cell is cut off, and almost simultaneously the fertilised carpogonium divides transversely to form a small superior cell and larger inferior cell (Fig. 3d). From the lower part of the latter a small cell ("connecting cell") is cut off which enlarges and grows out towards the auxiliary cell. The auxiliary cell elongates to meet the connecting cell and ultimately fuses with it (Fig. 3e–g). The zygote nucleus presumably is left in the inferior cell when the carpogonium divides and transferred via the connecting cell to the auxiliary cell. The other cells of the old carpogonial branch commonly contain more than one nucleus at this stage. The first, and less frequently the second and third, cells of the carpogonial branch may cut off one (rarely two) small cells which do not appear to have any function (Fig. 3e, f, h).

Comparatively few stages of actual fusion between carpogonium and auxiliary cell were found in comparison to large numbers of stages just before and shortly after, indicating that this transference of the diploid nucleus to the auxiliary cell is a rapid one.

The old carpogonial branch slowly disintegrates while the auxiliary (fusion) cell develops rapidly. Fusions between the auxiliary cell and other cells do not occur, but the auxiliary cell divides into a lower foot cell and upper central cell (Fig. 3h). The central cell buds off successive gonimolobes, each cutting off cells which divide to produce rounded groups of carpospores (Fig. 3i–l, Fig. 4). Only one fairly mature group of carpospores is present at any one time, with one or two younger groups developing. Mature carpospores average 75–80 μ wide by 100–120 μ long.

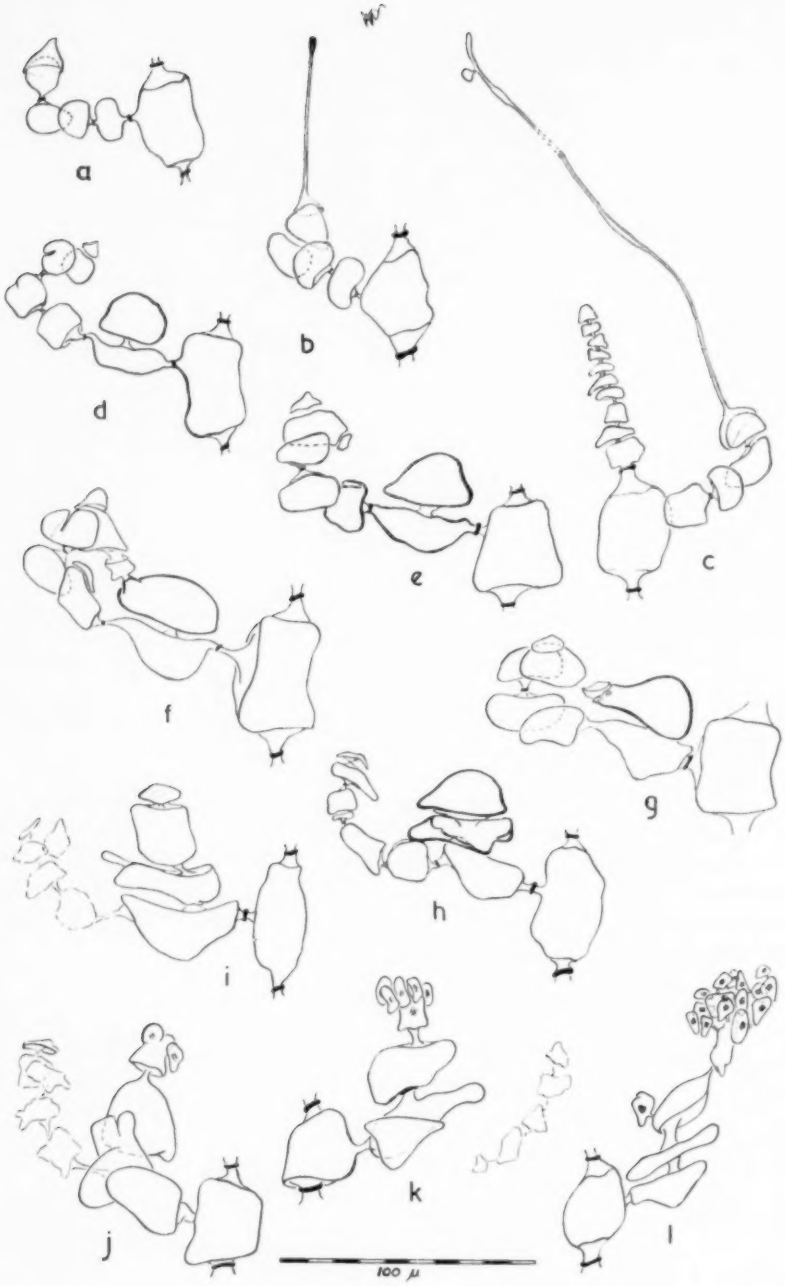
Two or three of the axial cells directly below those bearing carpogonial branches each bear a whorl of di- or trichotomously branched sterile filaments, which form a short, loose involucre around the carpospores (Fig. 4).

The mature carpospore groups are visible as small protrusions scattered irregularly over the thallus. The age of the carposporophytes shows a steady progression from the younger to the older parts of the thallus. On any one plant, however, there is not a very great difference between the oldest and youngest stages present.

SYSTEMATIC POSITION

As indicated in the introduction, *Gulsonia annulata* has been variously classified in the Cryptonemiales, Nemalionales, and Ceramiaceae by different authors. Previous accounts of the genus were all limited by inadequate material for study.

This investigation shows that *Gulsonia* is closely allied to *Crouania*, and belongs in the tribe Crouanieae of the Ceramiaceae. The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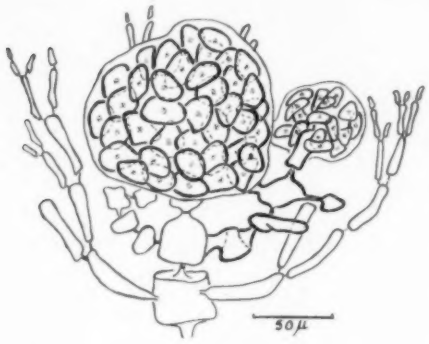

FIG. 4. Three stages in carpospore development. Sterile filaments from the axial cell immediately below the fertile axial cell form a loose involucre around the carpospore mass.

thallus construction, method of reproduction, and arrangement of the carpogonial branches are typical of the group. However, *Gulsonia* does differ from *Crouania* in two important features:

1. The carpogonial branches are borne on special fertile branches, whereas they are borne on the main axis in *Crouania*.

2. Lateral branches of unlimited growth are formed from the basal cell of a lateral whorl branch of limited growth, whereas in *Crouania* they develop directly from cells of the main axis.

These differences clearly indicate that *Gulsonia* is generically distinct from *Crouania*.

In 1940 J. and G. Feldmann separated *Crouania annulata* Berthold (a Mediterranean species) as a new genus *Crouaniopsis*, distinguished from *Crouania* by the same two features as distinguish *Gulsonia*. This separation, and J. and G. Feldmann's account of *Crouaniopsis* (see also Feldmann–Mazoyer, 1940) indicate that *Crouaniopsis* is generically identical with *Gulsonia* as has been recognised by Kylin (1956). In describing *Crouaniopsis*, Feldmann–Mazoyer (1940: 279) compares it with *Gulsonia*, noting the vegetative similarity of the two genera, but follows the description given by J. G. Agardh (1894) of the reproduction of *Gulsonia* and assumes the two to be generically as well as specifically distinct. Agardh's description is quite inadequate to indicate whether or not the two are generically distinct. The main features of *Gulsonia* (including *Crouaniopsis*) may be summarised as follows:

1. Thallus of uniaxial construction with short branches of limited growth in whorls of four from the upper part of each cell of the central axis, giving a noded appearance.

2. The development of young lateral branches of unlimited growth from the basal cells of the whorled laterals.

3. Four-celled carpogonial branches produced on special lateral branches which cease further development.

4. A short, loose involucre of filaments produced from axial cells at the base of the carposporophyte.

5. A loose cortication of the lower parts of the plant by filaments produced from the basal cells of the whorled laterals.

Gulsonia annulata Harvey and *Crouaniopsis annulata* (Berthold) J. and G. Feldmann are remarkably similar in form and appearance, but (judged from Feldmann–Mazoyer's figures and description) differ as follows:

FIG. 3. *Gulsonia annulata*. Stages in the development of the carposporophyte: a, Young four-celled carpogonial branch and supporting cell borne on axial cell of a fertile branch; b, trichogyne developing from the fourth (carpogonial) cell of the carpogonial branch; c, fusion of spermatia with fully developed trichogyne; d, stage after fertilization. Carpogonial cell divided and auxiliary cell cut off from upper face of the supporting cell; e, small connecting cell cut off from inferior carpogonial cell and elongation of auxiliary cell towards it; f, connecting cell fused with auxiliary cell while still attached to the inferior carpogonial cell; g, further fusion of connecting cell with auxiliary cell now completely separated from carpogonial cell; h, fusion cell (old auxiliary cell plus connecting cell) divided transversely to give an inferior foot cell and a superior central cell; i, first gonimolobe developed from central cell; j, first divisions in carpospore development from gonimolobe; k, further development of carpospores from gonimolobe; l, a second gonimolobe bud developing from central cell, while first bud continues further carpospore development.

1. The ultimate cells of the whorled laterals in *Crouaniopsis* are more elongate than in *Gulsonia annulata*.

2. *Gulsonia annulata* forms "gland" cells; *Crouaniopsis* apparently does not.

3. Tetrasporangia of *Gulsonia annulata* are formed on cells of the third order of the whorled laterals; in *Crouaniopsis* on cells of the second order.

4. In *Crouaniopsis* the spermatangia have an apical nucleus (Feldmann–Mazoyer 1940: 166), while in *Gulsonia annulata* the nucleus is median.

Direct comparison with preserved material of *Crouaniopsis* may show other differences, but they are clearly specifically distinct. Owing to the identity of the specific names, Kylin (1956) renamed the later species of Berthold. The genus *Gulsonia* thus comprises two species:

GULSONIA Harvey 1855

Gulsonia annulata Harvey (1855 : 334; 1860: 320, pl. 193A; 1863 : synop. 614). J. G. Agardh (1876 : 88; 1894 : 122, pl. II, f. 13; 1897 : 56). Kuetzing (1866 : pl. 66 c – e). De Toni (1897 : 66; 1924 : 151). Schmitz (1889: 435–456). Schmitz and Hauptfleisch (1897 : 329 – 331). Womersley (1948 : 161; 1950 : 178). Feldmann–Mazoyer (1940 : 279). Kylin (1956: 373).

DISTRIBUTION: Eucla, Western Australia to Georgetown, Tasmania.

Gulsonia mediterranea Kylin (1956: 373).
SYNONYMY: *Crouania annulata* Berthold (1882:518); *Crouaniopsis annulata* (Berthold) J. and G. Feldmann (1940: 181).
DISTRIBUTION: Western Mediterranean.

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A Mechanism of Color Variation Operating in the West Coast Sea Hare, *Aplysia californica* Cooper

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THE WIDE VARIATION in the coloration of different specimens of *Aplysia californica* Cooper, which inhabits the algal zones from Monterey Bay on the central California coast to the Gulf of California, has been the source of considerable question as to the specific homogeneity of the species. Cockerell (1901) based a new species name, *A. ritteri*, on an especially brightly colored variety. Garstang (1890) experimented with the European *Aplysia* and showed that there was a definite connection between diet and coloration. He believed that the veliger larvae settled in deep water and then migrated from deep water through the red, brown, and green algal zones, taking in turn the color of each.

MacMunn (1899) and Schreiber (1932) have indicated that the normal skin pigment is basically made up of degradation products of the tetrapyrrole molecule of chlorophyll. These are partly porphyrins, which are cyclic tetrapyrrole compounds, and bilins, which are linear chains of pyrrole molecules resulting from a break in the cyclic tetrapyrrole ring. The color and consequent absorption spectrum of these products varies as their structure is changed. Thus bilins from degraded green chlorophyll can produce a variety of blues, browns, greens, yellows, and reds which are all characteristic colors of the bilin compounds.

Many marine algae possess a high concentration of nonchlorophyllic pigments. Among these are the plant bilins or phycobilins, such as red phycoerythrin and the blue-green phycocyanin.

The colors most often seen in the skin of *A. californica* are brown, green, red, and purple, all of which are characteristic bilin colors. The purple pigments are concentrated in the branchial region and are seldom if ever seen elsewhere externally. The basic external body colors are brown, dark green, and grey, with various gradations between them. The red coloration is usually observed in larger specimens from deeper water and is the color most readily proved to be a result of food consumption.

In an effort to determine the relation of color to food, three approaches to the problem were used: (1) the comparison of color pattern and food, as shown by fecal pellet analysis; (2) controlled feeding experiments; and (3) observations on the absorption spectrum characteristics of the pigments.

MATERIALS AND METHODS

Juvenile specimens of *Aplysia californica*, ranging from 4 to 5 inches in length, were captured in the central shore area of Lunada Bay, Palos Verdes, California, and placed in individual pint fruit jars. As soon as a specimen passed a fecal pellet the pellet was collected in a vial and the animal was released in an area far enough removed so as not to be recollected. In this manner a total of 25 individuals was sampled. Pellets were also taken

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from large adult specimens from deeper water in Lunada Bay and off Palos Verdes Point, ¼ mile to the north. The pellets were collected in small, screen-capped vials, and were kept in refrigeration until they could be examined and tabulated.

Numerous specimens of *Aplysia californica* of various color combinations were kept from one to three months in 5-gallon pyrex cylinders supplied with aeration and glass wool–charcoal filters. The sea water was changed as pollution made necessary. These animals were fed on special diets to determine associated color relationships.

Hemolymph was drawn from the hemocoel after the animals had been cooled to refrigerator temperature to render them inactive. This prevented the release of the contaminating purple ink. The blood was centrifuged to remove the cellular elements, and the spectra were run on a Beckman model DU spectrophotometer. Extracts of the pigment of *Plocamium pacificum* were made by grinding the seaweed in a mortar with centrifuged sea hare hemolymph to duplicate the ionic conditions of the purple hemolymph occurring in certain specimens.

Extractions of certain dermal pigments were made with weak hydrochloric acid. Usually 10 per cent v/v was used, although one drop of concentrated hydrochloric acid in 10 cc. of distilled water would dissolve the pigment. The areas of the animal surface from which it was desired to extract pigment were cut off with scissors and placed in the dissolving solutions. These were then studied spectrophotometrically.

EXPERIMENTAL DATA

Fecal Pellets Analysis

The diet of the young specimens of dark green and grey coloration consisted of a wide variety of algae, but the dominant representatives were *Ceramium eitonianum* and *Gigartina canaliculata*. In no case was *Plocamium pacificum* present in noticeable quantity. All of the older specimens had red body streaks and a characteristic purple foot. In every case a varying but very noticeably dominant representation of *Plocamium pacificum* was found to be present. Other greener seaweeds were also present in small quantities.

Controlled Feeding Experiments

Specimens of *Aplysia californica* in all of the available color patterns were kept in the aquaria from one to three months and fed on a diet of parsley leaves and celery tops. These specimens all acquired a uniform pigmentation characterized by a light-brown base color and small dark-brown spots. One large feeding of *Plocamium pacificum* fed to these specimens produced a decidedly pink cast to the base color. This, however, was only temporary.

Two small red animals (2–3 inch) from the *Plocamium* beds north of Palos Verdes Point, apparently similar to the animals mentioned by Berry (1907), were kept in tanks in the laboratory. When captured, these young sea hares were a uniform light pink without markings, although one had a very few pinpoint dots of brown. These animals thus bore no color resemblance to the greenish-brown or red-streaked *Aplysia*. It appeared at first that they constituted a new species, but after two weeks of feeding on parsley leaves they developed the coloration characteristic of *A. californica*. These two animals, fed on parsley leaves, grew to be 4 to 5 inches in length and so closely resembled other animals of similar size and experimental diet but of different initial coloration that it became impossible to differentiate them.

Observations on the Pigments

The blood, or hemolymph, of *Aplysia* is normally a clear fluid without noticeable coloration. However, it was found that specimens feeding principally on *Plocamium pacificum* possessed blood with a strong purple coloration. Spectrophotometric curves were run on the blood and compared with extracts of *Plocamium;* however, while the curves themselves proved interesting, they did not show common absorption maxima with those found

in extracts of *Plocamium pacificum* nor did they show a relationship with *Aplysia* purple.

It was also noted that several hours after removing a dead *A. californica* from sea water, the brown epidermal layer of the skin can be rubbed off. In the red-streaked, *Plocamium*-feeding animals it was found that beneath this layer, on the surface of the unpigmented dermal layer, were broad, purplish red streaks of deposited material. In life these streak marks appear red, as the result of the filtering action of the thin epidermal layer. These streaks interconnect to form a reticulum which is most pronounced on the sides, especially near the margin of the foot.

The streaks were rapidly dissolved in dilute hydrochloric acid, dilute acetic acid, and 70 per cent alcohol, the latter changing the gross color to yellow. The acid extract consistently gave a strong absorption peak at 548 mμ (Fig. 1C) with an irregularity in the curve at 490 mμ. The nature of this irregularity suggested to the writer that the curve might be a composite. The streaks were differentially extracted with distilled water and dilute hydrochloric acid. In the former the streak-coated tissue was soaked overnight. The resultant extract was a light yellow and the gross color of the streaks had changed somewhat. The streaks were then completely dissolved in dilute hydrochloric acid in a few minutes.

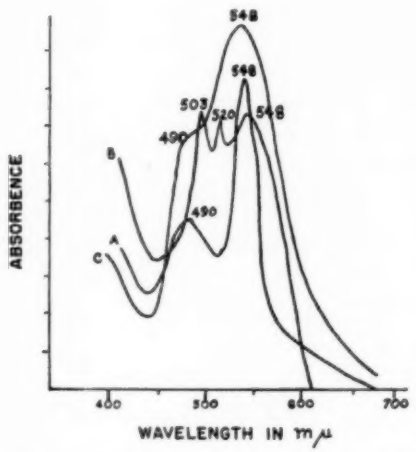

FIG. 1. The curve shown in A is produced by the water soluble fraction of the subcutaneous purple streaks, while that in B is produced by a subsequent acid extraction. The total spectrum of the two components is shown in C. No attempt was made to make the several extracts quantitative.

The water extract showed peaks at 548 and 490 mμ (Fig. 1B). The acid solvent contained a component with absorption maxima at 503, 520, and 548 mμ, the one at 548 being broad, the other sharp (Fig. 1A). No attempt was made to employ quantitative techniques so the relative height of curves A and B are probably not correctly portrayed. When the two are dissolved together the additive effect produced the curve in Figure 1C.

Upon neutralizing the composite extract of the streaks, the color completely disappeared. Upon reacidification the color was reconstituted without significant spectral change, but if made strongly alkaline, a jell-like precipitate formed.

DISCUSSION AND CONCLUSIONS

The reversion of specimens of all available color patterns to a common pigmentation when fed a common diet demonstrated the dependence of these animals on food pigments for their coloration. The land plants which supplied principally chlorophyll as a pigment lacked the special pigments which are normally obtained by these animals from their algal diet. It seemed logical to search for the cause of the red streaks from among these special algal pigments.

The consistence with which *Plocamium pacificum* was found in the fecal pellets of the red-streaked animals led to experiments with that algal form. Feeding experiments involving *Plocamium* over the extended period necessary to produce red streaks were impractical because of the perishable nature of the sea weed. However, single large feedings produced a pinkish cast on the bodies of parsley-fed experimental animals, caused by the blood's becoming temporarily purple.

The lack of common absorption maxima between the extracts of *Plocamium pacificum* and the purple-colored blood is doubtless the result of digestive changes. The significant fact, however, remains that animals feeding on the pinkish purple, phycobilin-pigmented *Plocamium pacificum* develop purple hemolymph. The fact that these purple-blooded specimens also lay down a subcutaneous purple reticulum is very significant, showing the manner in which this particular pigment is transferred from plant to animal pigmentation. It has been demonstrated that the portion of the streaks insoluble in water was soluble in hydrochloric acid. This solubility characteristic suggests the presence of a nitrogen base, perhaps an amine.

SUMMARY

1. Fecal pellet analysis indicated that *Plocamium pacificum* is the major dietary component of red-streaked *A. californica*.

2. The coloration of the widely different color variants could be changed to a homogeneous, indistinguishable pattern by feeding them a diet of parsley and celery leaves.

3. The absorbed pigment from the digested *Plocamium* colors the blood of the sea hare purple.

4. A pigmented compound may then be deposited in a subcutaneous, purple reticulum, having the gross effect of red streaks due to the filtering action of the brown cutaneous layer.

5. Though all the pigments in the chain are of a red to purple color, they have been so changed in the body of the sea hare as not to have common absorption maxima. Their spectra show no affinity with *Aplysia* purple.

6. The streak deposit is composed of not less than two component pigments.

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Four New Species, a New Genus, and a New Suborder of Hawaiian Fishes[1]

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THE DESCRIPTION of new taxa in a "Handbook of Hawaiian Fishes" recently submitted for publication was considered inadvisable. Certain of these are grouped together here, i. e., three new species of Gobiidae (*Quisquilius aureoviridis*, *Q. limbatosquamis*, and *Hazeus unisquamis*), a new genus and species of Callionymidae (*Pogonymus pogognathus*), and a new suborder of Perciformes (Schindlerioidei) erected for the fishes of the genus *Schindleria*.

Family GOBIIDAE, Genus QUISQUILIUS

The two new species of *Quisquilius* described below can be assigned to that genus with considerable assurance, as the type species, *Q. eugenius*, is another Hawaiian form of which numerous specimens are available. The characteristics listed in the following paragraph are held in common by the two new species and *Q. eugenius*.

No hairlike or flaplike appendages on the head or shoulder girdle. No serrations or spines on the preopercle. Maxillary not prolonged posteriorly. No V-shaped notch in the tip of the lower jaw. No teeth on the vomer. Teeth in both jaws in several rows, those of the outer and inner rows enlarged and spaced at intervals. One or two fanglike teeth in the outer row at each anterolateral angle of the lower jaw. Tongue usually with a slight to broad notch in the tip. Cleft of the mouth more or less oblique. Both nostrils in tubes, the anterior at least twice as far from the posterior as from the groove behind the upper lip. No pores on the head. The rows of papillae (not shown in Fig. 2) are in very uniform alignment. There is one pair on the posterior portion of the interorbital and two rows of about 5 papillae each on the flesh covering the premaxillary pedicels. A series of about 5 large, widely spaced papillae borders the orbit below. A row or pair of rows runs backward from the eye just above the upper border of the opercle. Two horizontal rows on cheek, the upper sometimes extending all the way across but the lower ending on middle of cheek. A verticle row down front of operculum with two branches running back or down and back from it. One or two rows along the lower border of the preopercle. One row of papillae above and two below enclose the corner of the mouth. Two rows on the gular membrane, one on each side. Gill openings extending down to below the preopercular border, the distance between their lower ends equal to or less than an eye diameter. Ten or more developed gill rakers on the lower limb of the outer arch. Scales ctenoid, those on the body not especially enlarged posteriorly. Scales on top of head extending forward nearly to eyes, but no enlarged scales just behind eyes. First dorsal fin with 6 spines. First spine in both dorsal fins with a flexible tip. Caudal rounded, not longer than the head length. Pectoral without silky rays above. The united pelvics without a basal frenum, the membranes uniting the inner rays easily torn (as it apparently was in the holotype of *Q. eugenius*).

Examination of numerous specimens of *Q. eugenius*, 15 to 45 mm. in standard length, indicates no great sexual dimorphism. Over the available size range there is also no great differentiation in sensory papilla pattern. However, the cheek squamation does not appear until well after all of the other scales have formed.

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Among Hawaiian gobies *Zonogobius* (as represented by *Z. farcimen*) seems to be the closest relative. These two genera are set off from other Hawaiian gobies by the following features: no pelvic frenum; two longitudinal series of papillae on the flesh covering the premaxillary pedicels; and 10 or more developed gill rakers.

Of the three Hawaiian species of *Quisquilius*, *Q. eugenius* is an abundant shallow-water fish inhabiting areas of dead coral. It seems to be restricted to depths of less than 15 feet. The other two species are in general deeper-water forms, though the type of *Q. aureoviridis* was collected in a tide pool with a maximum depth of 7 feet.

Quisquilius aureoviridis sp. nov.
Fig. 1, Table 1

HOLOTYPE: USNM 175013, 37.1 mm. in standard length taken in a rotenone station at Pupukea, Oahu, Territory of Hawaii by Gosline, *et al.*, Dec. 23, 1949.

PARATYPES: USNM 175014, 1 specimen. 36.2 mm., about 1 mi. north of Kailua, Hawaii, T. H., Gosline, *et al.*, June 19, 1953; University of Hawaii No. 1703, 8 specimens, 21.0–27.2 mm., off Waikiki reef, Oahu, T. H., Gosline, *et al.*, Dec. 31, 1952.

Depth of body contained about 4 times in the standard length.

Head somewhat wider than deep, its greatest depth contained about 1.5 times in the head length. Mouth oblique, the lower jaw protruding. Front of mouth about on a level with the middle of pupil; rear of jaw about reaching to below front border of pupil. Eye bordered by a shallow groove posterodorsally, its diameter contained about 4 times in head in a 2-inch specimen. Least distance between eye and groove behind upper lip contained a little over 2 times in the eye diameter. Anterior nostril placed just above the groove behind upper lip, the posterior above the level of the top of pupil. Interorbital gently concave, not in a deep trench between the eyeballs, its width contained about 4 times in the eye diameter. Thirteen moderate, pectinate gill rakers on the lower limb of the outer arch in one specimen. Tongue rounded but usually with a central notch at tip.

Body completely scaled, those scales above the pectoral base rather irregularly placed. A few scattered rows of papillae crossing certain of the body scales. Head scaled forward to the groove behind each eye. No scales on cheek or operculum. Thirty to 33 scales in a longitudinal series, 9 or 10 in a transverse series; about 13 predorsal scales.

Some of the spines in the first dorsal filamentous. Second dorsal with a spine and 10 or 11 soft rays. Anal with a spine and 8 or 9 soft rays. Pectoral with about 19 rays.

TABLE 1
CERTAIN COUNTS IN THREE HAWAIIAN SPECIES OF *Quisquilius*

SPECIES	LATERAL LINE SCALES*								TRANSVERSE SCALE ROWS†					TOTAL 2ND DORSAL RAYS				TOTAL ANAL RAYS		
	26	27	28	29	30	31	32	33	7	8	9	10	11	10	11	12	13	9	10	11
Q. eugenius		1	1	3							2	2	1			4	1	1	3	1
Q. aureoviridis																				
Holotype								1				1				1			1	
Paratypes				1	1	1		1			3	2			2	3		3	2	
Q. limbatosquamis																				
Holotype		1							1						1			1		
Paratypes	2	4							3	3				6				5	1	

* Counted from the upper angle of the gill opening to the crease at the end of the hypural fan.
† Counted from the beginning of the anal upward and forward to the dorsal base.

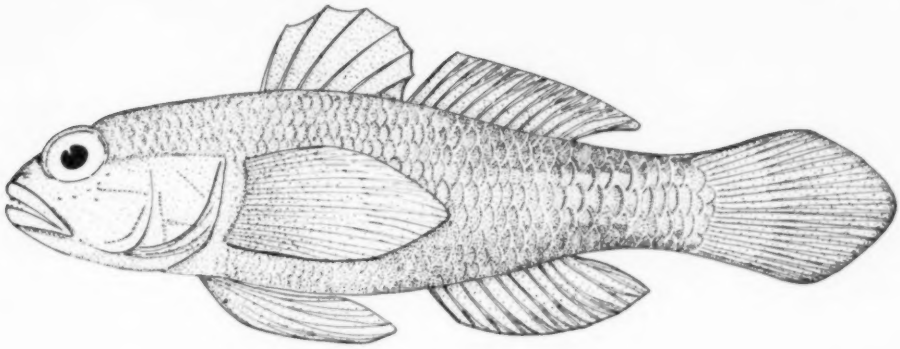

FIG. 1. *Quisquilius aureoviridis*, holotype.

Color in life yellowish green to yellowish brown with faint slightly darker vertical bars. In alcohol a broad, lighter longitudinal bar becomes apparent along the middle of the body posteriorly. Fins light or dusky. Small specimens show traces of dark vertical bars on the head.

Quisquilius aureoviridis differs from *Q. eugenius* most notably in interorbital structure. In the latter species the eyes are raised, leaving a deep, narrow trench between them, the bottom of which is hardly visible; in *Q. aureoviridis* the eyes are little raised above the level of the relatively broad interorbital. In *Q. eugenius* the scales on the cheek and opercle are prominent in adults; in *Q. aureoviridis* they are absent. Finally, the two species may at once be separated in life by coloration, for *Q. eugenius* is a brownish black with vertical stripes.

Koumans (1953: 131) has synonymized four other species with *Q. eugenius*. Of these, three at least—*Q. cinctus*, *Q. naraharae*, and *Q. profundus*—do not seem to belong there. They appear, on the contrary, to be somewhat nearer *Q. aureoviridis* at least in the lack of squamation on the cheek and (usually) on the operculum. All of them differ from *Q. aureoviridis*, however, in having the body dark with light bands and in the punctate soft dorsal and anal fins.

Quisquilius malayanus and *Q. macrophthalmus* appear to be relatively large scaled forms, as is the species described below.

Aureoviridis = (L.) yellow green.

Quisquilius limbatosquamis sp. nov.
Fig. 2, Table 1

HOLOTYPE: USNM 175012, 20.0 mm. in standard length, taken in a rotenone station about 2 mi. west of Haleiwa, Oahu, Territory of Hawaii by Gosline, *et al.*, July 23, 1955.

PARATYPES: University of Hawaii No. 1704, 8 specimens, 15.6–18.5 mm., off Waikiki reef, Oahu, T. H., Gosline, *et al.*, Dec. 31, 1952.

Depth of body contained 4.5 times in the standard length.

Greatest width of head considerably greater than greatest depth of head, the latter contained about 1.9 times in the head length. Mouth oblique, the lower jaw protruding. Front of mouth about on level with center of pupil. Rear of jaw below front of pupil. Eye not surrounded by a recessed groove above or posteriorly, its diameter contained about 3.7 times in the head length. Smallest distance between eye and groove behind upper lip contained about 2.5 times in the eye diameter. Anterior nostril about ⅓ as far from the groove behind upper lip as from the posterior nostril. Posterior nostril slightly above top of pupil. Interorbital narrow, not in a deep recess, its width contained perhaps 5 times in

the eye diameter. No pores on head. Rows of papillae on head less markedly developed than in *Q. aureoviridis*. Ten gill rakers on the outside row of the lower limb of the first arch. Pseudobranch composed of 4 lobes. Tongue as seen from below rounded but with a slight indentation in middle.

Body completely scaled except apparently on the middorsal ridge that runs about one eye diameter forward from the first dorsal fin. Head scaled forward to an imaginary line drawn across between the rear of the orbits. Cheek and opercle scaleless. Twenty-six or 27 scales in a longitudinal series; 7 or 8 transverse rows; predorsal scale row incomplete. Scales ctenoid, except perhaps for those on breast.

None of the dorsal spines filamentous. Membrane between the two dorsals not quite connecting them. Second dorsal with a spine and 9 or 10 rays. Anal with a spine and 8 rays. Pectoral 19 or 20.

Color light with a light, dark-bordered vertical band crossing the nape and enclosing the pectoral base. Behind this are 6 vague dark vertical bands, one of these at caudal base, the others darkest on the middorsal and midventral lines. Each scale on the body completely and prominently outlined by a series of large melanophores. Dorsal fins, particularly the first, with dark smudges at the base of the rays. Soft dorsal rays speckled. Head with traces of 3 broad vertical bands running down cheek and operculum.

This species was taken along with *Quisquilius aureoviridis*. It resembles that species rather than *Q. eugenius* in that the orbits are not partially enclosed in a deep trench and in the absence of scales on the cheek and head. However, *Q. limbatosquamis* differs from both the other Hawaiian species of the genus in the somewhat flatter head, in having a triangular naked area on the top of the head between and behind the eyes, in having a naked ridge extending forward from the first dorsal, in the larger scales and fewer dorsal rays. In color *Q. limbatosquamis* differs from the other two in having each of the scales distinctly outlined by a series of melanophores.

Of other described species *Q. limbatosquamis* seems to differ from *Q. malayanus* in color and from *Q. macrophthalmus* in the far higher pectoral count.

Limbatosquamis = (L.) edged scale.

Family GOBIIDAE, Genus HAZEUS

The relationships of the fish described below are most obscure, at least to the present author. It has been placed in the genus *Hazeus* because nothing better could be found. As one source of confusion this author has never seen the type species of *Hazeus*, *H. otakii* Jordan and Snyder (1902: 51, fig. 3). As another, the genus has frequently been considered a synonym of *Gnatholepis*, e.g., by Jordan and Evermann (1905: 487) and by Koumans (1931: 86; 1953: 168), but until it can be determined what fish *G. anjerensis*, the type species of *Gnatholepis*, represents there can be no final decision on the matter.

Hazeus unisquamis sp. nov.
Fig. 3

HOLOTYPE: USNM 175009, 18.2 mm. in standard length, taken by means of rotenone in a cut in the reef about 200 yds. west of Diamond Head, Oahu, Territory of Hawaii, by Gosline and class, May 16, 1950.

Depth of body contained 4 times in the standard length. Depth of caudal peduncle contained about 2.5 times in its length.

Head considerably wider than deep, the greatest depth of head contained about 1.4 times in the head length. Cleft of mouth broad and very slightly oblique, the lower jaw somewhat projecting. Front of mouth about on a level with lower border of pupil; maxillary reaching to below middle of eye. Upper lip narrow, its greatest width somewhat less than that of lower lip. Eye directed superolaterally, its diameter contained about 2.2 times in the head length. Smallest distance between eye and groove behind upper lip contained about 4 times in the eye diameter. Both

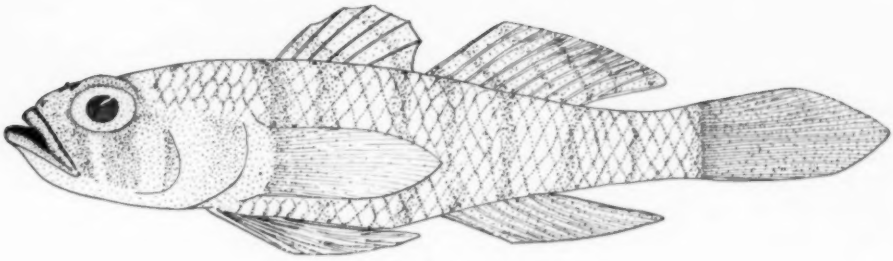

FIG. 2. *Quisquilius limbatosquamis*, holotype.

nostrils bordered by a low, raised collar, the anterior slightly nearer the posterior than the groove behind upper lip. Interorbital very narrow, hidden in a groove between the raised orbital borders. No pores on the head. Superior borders of orbit raised in a series of low flaps, these bordered behind by a groove; behind the interorbital region this groove is also bordered on the side away from the eye by a series of raised, scalelike flaps. No papillae on top of head, snout, or around eye, but two rows following the lower portion of the preopercular border and extending forward below the ramus of the lower jaw; another weakly developed vertical row on anterior portion of operculum. Gill cover free from the isthmus, the gill openings extending far forward about to below front of pupil. Ten widely spaced, pectinate gill rakers on the lower limb of the outer arch. Pseudobranch consisting of 5 lobes. Tongue with a broad, shallow median indentation as seen from below. Teeth in a narrow band in both jaws, some of the teeth on the inner border of the band somewhat enlarged; none of the outer teeth in either jaw especially enlarged.

Top of head scaled forward to the eye. Operculum almost completely covered by about 12 large, ctenoid scales. A single, large, embedded scale on the upper portion of each cheek. Twenty-six scales in a longitudinal series from above the upper end of the gill cover to the base of the caudal; 6 scales in a transverse series. Breast in front of pelvics without scales.

All of the fins with short, heavy rays maintained more or less erect. First spine in both dorsal fins more slender than the succeeding rays and with a soft tip. Dorsal VI-I,7. Anal I,7. Pectoral without silky rays above, with 18 rays in all; the upper 11 rays branched, the lower 7 simple, swollen and extending somewhat beyond the interradial membranes. Pelvics united, with a thin, smooth-edged frenum anteriorly.

In alcohol the only prominent marks are narrow black borders to the two dorsal fins and a blackish bar across the caudal peduncle just in front of the caudal base; chromatophores are scattered more or less evenly over the rest of the body and head, giving a plain gray ground color.

So far as I can see from the species descriptions available to me *Hazeus unisquamis* may be differentiated from related forms by having only a single scale on the cheek, dark borders to the two dorsal fins, and only 7 soft rays in the dorsal and anal.

Unisquamis = (L.) one scale, in reference to the single cheek scale.

Family CALLIONYMIDAE

POGONYMUS gen. nov.

TYPE SPECIES: *Pogonymus pogognathus* sp. nov.

Head and body depressed forward of the anal origin, compressed posteriorly. Head flat above, the eyes completely separated by a slightly concave interorbital area. No supraorbital tentacle. Preopercular process with an

upturned tip and with one additional dorsally directed spine ahead of tip; without an antrorse spine on its outer surface. Gill opening a small hole beneath the dorsal portion of the well-developed opercular flap. Lower jaw included, without a reverted lip but with a fringe of about 12 to 16 forwardly projecting papillae the tips of which extend beyond the upper jaw when the mouth is closed. Teeth elongate, in one or a few rows in both jaws, those above pointing backward, those below projecting up and back. A single lateral line running along sides, without notable side branches except for one at the rear, which forms a saddle across the caudal peduncle. Two dorsal fins, the first very low, of 2, 3, or 4 spines none of which reach the second dorsal origin when the first dorsal is depressed. Rays of second dorsal unbranched except for the last. All of the anal rays branched at tip, except for the last, which is divided to the base. Pelvic fins without separated rays and not attached to the middle of the pectoral fins by a membrane.

Judging from the keys to callionymid genera given by Schultz and Woods (1948: 419–420) and others, *Pogonymus* is most closely related to *Eleutherochir*. It differs from that genus and most other callionymids in the presence of a fringe of papillae on the lower jaw and in having the anal, but not the soft dorsal, rays divided at the tips.

Pogon = (Gr.) beard; onyma = (Gr.) name.

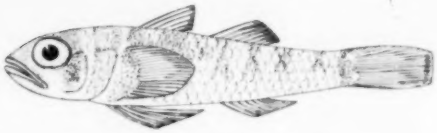

FIG. 3. *Hazeus unisquamis*, holotype.

Pogonymus pogognathus sp. nov.
Fig. 4

HOLOTYPE: USNM 175010, a nearly ripe female 25 mm. in standard length, taken in 3 to 10 ft. of water in a small cove just west of Hanalei Bay, Kauai, Territory of Hawaii, by Gosline and Ohai, June 19, 1952.

PARATYPES: USNM 175011, 5 specimens, 15–21 mm.; University of Hawaii No. 1626, 34 specimens, 11–22 mm., all with the same data as the holotype.

Head broad and flat, its greatest depth contained about 1.6 times in its greatest width, which in turn is contained about 1.2 times in the head length to the end of the opercular flap. Eyes large, contained about 4 times in the head length, not projecting above the dorsal surface of the head, separated by a bony interorbital that is about equal to a pupil diameter in width and that contains two median pores. Snout broad and blunt, its length about ⅔ an eye diameter. Gape nearly twice as broad as deep, the maxillary reaching about to the anterior border of the eye when the mouth is closed. Gill covers attached to one another below by a free fold across the isthmus.

Lateral line dropping down to the midsides about at the pectoral tip, giving rise to about 15 pores along its length, some of these slightly above the lateral line and others slightly below; terminating posteriorly about halfway out along the caudal rays.

FIG. 4. *Pogonymus pogognathus*, paratype.

First dorsal originating about ⅓ of the way back along the standard length, its rays low and rather tightly bound to the midline of the back by the membrane behind the last ray. Longest dorsal spine considerably shorter than the distance between dorsal fins. Soft dorsal with 9 or 10 rays, lying somewhat ahead of anal, its last ray not nearly reaching caudal base when depressed. Anal with 9 or 10 rays, the tip of the last about reaching caudal base.

Caudal fin slightly shorter than the head length, with 6 principal rays, all of which are somewhat branched at tip, the outermost least so; 10 caudal rays in all, the outermost short, splintlike, and unsegmented. Pelvic fins with a spine and 5 branched rays, the fourth of which is the longest. Pectoral with about 19 rays, the longest of which reach about to above the anal origin.

A 15 mm. (standard length) specimen has black spots at the base of each soft dorsal and anal ray and another at the base of tail. Between 15 and 20 mm. these markings fade, so that the specimens are a plain yellowish brown except for some incipient markings on the back and on the first dorsal. At a length of 25 mm. the first dorsal is almost completely black, and there are prominent dark bars and spots symmetrically arranged on either side of the middorsal line on the body and head.

The three specimens sexed, 22 to 25 mm. in standard length, proved to be nearly ripe females. If adult males are represented among the types, they show no striking external differences.

The species has been taken only once. This was from a poison station run in a small, semi-protected cove in which a vertical, alga-covered ledge dropped vertically to a uniform sand bottom 3 to 10 feet below. *Pogonymus pogognathus* was the most abundant species taken. Whether the individuals were living on the ledge or in the sand below (as seems more probable judging from the fringed lip) was not verified at the time. Just how this habitat differed from that of innumerable other poison stations run from ledges dropping off to a sand bottom remains unknown to the author.

Pogon = (Gr.) bearded; gnathos = (Gr.) jaw.

Suborder SCHINDLERIOIDEI

The two known species of *Schindleria* (see Fig. 5) were first described as members of the genus *Hemiramphus* in the 1930's. They have been bounced about from order to order ever since. The members of the genus are neotenic

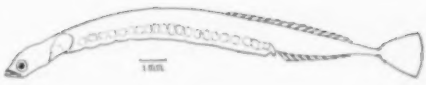

FIG. 5. *Schindleria praematurus*, female with eggs. (After Bruun.)

fishes, apparently without close relatives, which have lost the adult characteristics that would presumably indicate their relationships. The present erection of a new suborder of perciform fishes for *Schindleria* is not made on the basis of any decisive new material; it merely seems to be the best available solution to a difficult problem. Knowledge of *Schindleria* may be marshaled under four heads: neoteny, sexual differentiation, soft anatomy, and "osteology." These will be dealt with only in so far as they bear on the systematic position of the genus.

Neoteny: That a 20 mm. *Schindleria* may be sexually mature is often indicated by the conspicuous presence of large eggs in the females. That the rest of the fish is in a larval stage of development is shown by the presence of the atrium directly behind, i.e., on the same horizontal plane with, the ventricle (Schindler, 1932: pl. 4c); by what is apparently a functional pronephros (Schindler, 1932: 25); by the well-developed opercular gill (Schindler, 1932: 12); the tremendous, protruding eyes; the rounded pectoral fin attached to a lobate, fleshy base; the transparent body; and by the degree and nature of the "ossification" of the skeleton (see below).

Neoteny in fishes is rare, and nowhere is it carried to the extreme found in *Schindleria*. It is also apparently sporadic, occurring as it does in some of the Clupeiformes (e.g., Salangidae), in at least one member of the Beloniformes (*Cololabis adocetus*), and perhaps in the gobioid Perciformes. Consequently, its neotenous nature is of no great aid in the systematic placement of *Schindleria*. One is merely inclined to ask the irrelevant question why neoteny does not occur more often among fishes of the open ocean.

Sexual Differentiation: Aside from the primary sex organs there is in the males (but not the females) of *Schindleria*, especially in *S. praematurus*, a long urogenital papilla (Schindler, 1932: 6, 8; Bruun, 1940: 7, fig. 2). In addition, the anus of both species lies farther back along the body in females than in males (Schindler, 1932: 6, 8; Bruun, 1940: 5).

Soft Anatomy: In 1932 Schindler described the soft parts of *Schindleria praematurus* with special reference to the heart, swim-bladder, gills, and the digestive and urogenital systems. None of the features described, nor the sexual differentiation, provides the present author with any clue as to the taxonomic relationships of the genus.

"Osteology": There is some difficulty in determining what should be included under "osteology." Schindler (1932: 6) states: "An ossification or deposit of lime in the vertebrae is not present." However, the vertebrae take up alizarin stain. In the account of the osteology that follows all those portions that stain with alizarin will be considered "ossifications."

As the final comment in his paper on *Schindleria*, Giltay (1934: 10) has said: "Des matériaux plus nombreux nous permettront de mieux définir ses affinités, surtout quand on aura mieux pu étudier le squellette qui est deja relativement bien développé." There are several difficulties with this proposition. First, additional material has been gathered and it has not helped much. Second, the degree of ossification in the additional specimens is about the same as in those taken earlier, and there seems little hope of finding an adult-type ossification in *Schindleria*. Third, the "ossification" that is present occurs to approximately the same extent and in about the same areas as in a larval anchovy of the same size. To what extent this larval-type ossification in *Schindleria* is comparable to the bony structure of other adult fishes is an open question. (In this author's opinion, the "ossifications" that do occur in *Schindleria* are not of an adult fish type at all but are merely calcifications of normally larval structures. Indeed, it seems that the adult *Schindleria* has retained larval features which have to some extent "ossified" precociously as compared to the ontogenetic development of the same features in normal fishes. If this is true, the calcifications in *Schindleria* bear little comparison with normal adult fishes and are only incompletely comparable with any larval stage.)

Judging from the absorbtion of alizarin stain, the jaws, vertebral centra, and fin rays are the best ossified portions of *Schindleria*. The upper jaw consists of a toothed premaxillary and a toothless maxillary of about equal length (Fig. 6a). The premaxillary has an upwardly projecting flange a little more than halfway out. The premaxillary pedicel is broad and low, articulating medially with a large cartilaginous (?) median pad and laterally with the maxillary. The latter bone has an abrupt, sharp-angled bend (Fig. 6b) that hooks around the premaxillary pedicel; the bone then projects medially inside the pedicel.

The lower jaw consists, so far as can be determined, of a single ossification (Fig. 6e), though an obscure "suture" between dentary and articular may have been missed.

The suspensorium runs very obliquely forward in order to pass below the very large eye (Fig. 6c) between the skull and the lower jaw. The only portion of the suspensorium that takes stain is a long splint made up of the quadrate below and the hyomandibular above (Fig. 6e). From the rear of the hyomandibular projects an elongated, leaf-shaped operculum.

The hyoid apparatus (Fig. 6e) consists of a vaguely ossified glossohyal in front, an elongate ceratohyal, and an epihyal. The last bone loops around posteriorly to join the upper portion of the hyomandibular. There are 5 short branchiostegals; 2 on the ceratohyal and 3 on the epihyal. There are 4 gill arches (Schindler, 1932: 11); the lower pharyngeals are separate.

The forward portion of the cranium does not take up stain. To the rear above there are three small, partial ossifications which are here

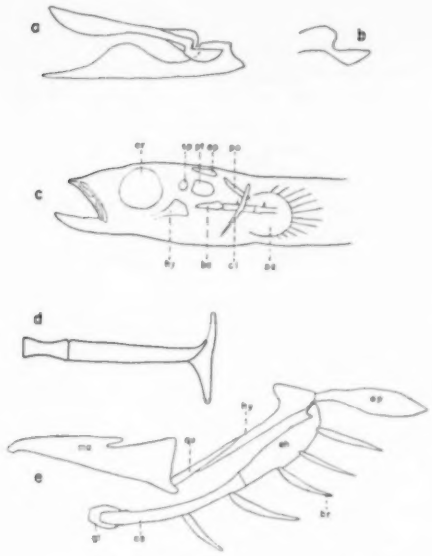

FIG. 6. *Schindleria*. a, Left premaxillary and maxillary from the inside, the posterior end of the maxillary somewhat raised. b, Median end of left maxillary from above. c, Head and fore part of body to show certain "ossifications." d, Caudal skeleton and posterior portion of "vertebral column." e, Mandible, suspensorium, opercle, and hyoid apparatus. ba, "Basioccipital"; br, branchiostegal ray; ce, ceratohyal; cl, cleithrum; eh, epihyal; ep, epiotic; gl, "glossohyal"; hy, hyomandibula; ma, mandible; op, opercle; or, orbit; pe, pectoral lobe; po, "posttemporal"; pt, pterotic; qu, quadrate; and sp, sphenotic.

provisionally identified as epiotic, sphenotic, and pterotic. Running in under the skull is a projection of the vertebral column which may represent the basioccipital (Fig. 6c); a possible alternate interpretation of this "bone" is suggested below.

The pectoral girdle consists of two simple struts (Fig. 6c) representing the cleithrum and probably the posttemporal. There is nothing in the fleshy lobe between the cleithrum and the pectoral rays that absorbs alizarin stain.

The vertebral centra stain clearly but the neural and haemal arches seem to be represented only by short spines that ride on the centra. The number of differentiated vertebrae vary from 33 to 39 in the genus (Schindler, 1932: 6, 8). At the rear of the vertebral column is a rodlike structure with an upturned tip that runs for the length of about 3 normal vertebrae. To its posterolateral face is attached a plate (Fig. 6d). Both of these features take stain well.

Since it is this terminal portion of the axial skeleton that forms the feature of *Schindleria* unique among all known fishes, some discussion of it seems in order. The terminal plate would appear to take the place of the hypural fan, differing from the usual caudal skeleton in the complete lack of separate ossifications. The rodlike portion of the "vertebral column" ahead of it is difficult to interpret satisfactorily. When the vertebral column first ossifies in an anchovy, the caudal portion of the column forms early as a number of small elements which eventually fuse to a considerable extent to form the adult caudal skeleton. One presumes that the tail rod of *Schindleria* evolved in a different ontogenetic fashion. The most satisfactory explanation for it that the author can find is that it represents the posterior portion of the notochord which has been replaced by cartilage and/or bone without dividing into discrete vertebral segments.

In this connection it is necessary to revert to the skull bone that was provisionally called the basioccipital in earlier paragraphs. The alternative explanation is that it is the forward end of this same notochord which has taken up stain in the same way suggested for the posterior rod.

In the caudal fin there are 13 rays, 11 of which are branched. The interneurals and interhaemals of the dorsal and anal fins respectively bear a one-to-one relationship with the vertebrae (see Bruun, 1940, fig. 2). There are from 15 to 20 unbranched dorsal rays, and from 11 to 17 unbranched rays in the anal; the pectoral contains 15 to 17 rays (Schindler, 1932: 7, 8).

Relationships: As mentioned, *Schindleria* was first described as a neotenic *Hemiramphus*.

Giltay (1934) demonstrated the incorrectness of this allocation. *Inter alia*, *Schindleria* differs from all of the Beloniformes in the low number of branchiostegal rays, the absence of fused pharyngeals, and the one-to-one relationship between dorsal or anal fin rays and vertebrae.

A rather better case could be made for placing *Schindleria* in the Syngnathiformes or Gasterosteiformes. However, the Syngnathiformes are characterized by having the first 3 to 6 vertebrae immovably united. The lack of a tubular snout, of external bony plates, and of a soft dorsal fin with closely spaced rays argues against placing *Schindleria* in either of these orders.

Turning from negative to positive indications of relationships, there appears to be only one character in *Schindleria* which provides any clues. This is, as already noted by Giltay (1934), the one-to-one relationship between the dorsal or anal fin rays and the vertebrae. It appears that this characteristic is limited to the Perciformes, being found there in the trachinoid, ammodytoid, blennioid, and many of the gobioid fishes. However, the basal perciform stock has, like other fishes, two or three soft dorsal and anal rays (with their interneurals and interhaemals) per vertebra. Just why certain perciform groups should have a one-to-one relationship between these features remains unknown. That it is a polyphyletic development is shown by the gobioid fishes, where this relationship seems to have developed within the group itself. At least, *Pterelеotris* has the usual two or three interneurals per vertebrae whereas most of the other gobioids have only one (Gosline, 1955: 166). If the one-to-one relationship has occurred several times within the perciform fishes, could it not also occur within other orders? The best available answer to this question seems to be that it apparently has not done so.

To sum up regarding the ordinal position of *Schindleria*, the genus seems to rest most easily (or rather least uneasily) among the Perciformes. There is nothing to really invalidate such a position and there is the one-to-one fin ray to vertebra relationship to recommend it. Where *Schindleria* belongs among the Perciformes is obscure. The best that can be done is to place *Schindleria* in the neighborhood of the blennioid fishes.

The reason for raising *Schindleria* to subordinal rank (rather than placing it in the Blennioidei as Giltay, 1934, has done) lies in the rodlike terminal section of the spinal column. There seems to be nothing like it elsewhere in fishes. The author has looked through the literature on both adult and larval fishes without finding anything similar. He has discussed this precaudal rod with E. A. Ahlstrom, A. F. Bruun, and C. L. Hubbs, and wishes to thank them for their help on this matter; nevertheless, nothing resembling this rod has come to light. In the great majority of modern fishes the notochord is replaced by vertebrae. However, when this occurs the vertebral replacement runs all the way back to the caudal skeleton. The uniqueness of *Schindleria* lies in the fact that vertebral development stops short some distance before the caudal skeleton.

There is one other feature of *Schindleria* that this author has never encountered elsewhere in fishes or in the literature (although this may simply indicate a gap in the author's knowledge, especially in regard to larval fishes). In *Schindleria* the hyoid apparatus (Fig. 6) articulates with the upper head of the hyomandibular. In all the fishes the author knows, the hyoid apparatus articulates by means of the interhyal at the lower extremity of the hyomandibular.

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A New Species of Polychaetous Annelid (Family Capitellidae) from Southern California[1]

DONALD J. REISH[2]

DURING THE COURSE of studying the quantitative distribution of polychaetous annelids in Newport Bay, California, a new species belonging to the capitellid genus *Scyphoproctus* Gravier 1904 was encountered. This is the first report of the genus in the eastern Pacific Ocean.

Only two species of this genus have been reported previously. *Scyphoproctus djiboutiensis* was described from the Red Sea by Gravier (1904, 1906), and subsequently was reported from India by Fauvel (1930, 1953). Okuda (1940) described *S. gravieri* from Okinawa.

The author wishes to express his thanks to Dr. Russell Cangialosi for his assistance with the drawings.

Scyphoproctus oculatus n. sp.

A total of 28 specimens was collected from the bottom of Newport Bay, California, with a size one Hayward orange-peel bucket. These stations were all located near the Pacific Coast Highway (Alternate 101) Bridge which passes over Newport Bay.

The holotype measures 20 mm. in length and 1.0 mm. in width. Other complete specimens ranged from 8 to 20 mm. in length. The prostomium (Fig. 1) is broadly rounded in front and bears one pair of elliptical-shaped eyes on either side. The peristomium lacks setae. The following 12 segments are setigerous with only simple capillary setae (Fig. 2) in both the notopodium and neuropodium.

The abdominal region of the holotype consists of 85 setigerous segments. Hooded hooks (Fig. 3) are present in both the notopodium and the neuropodium of each segment, except at the posterior end (see below). The hooks bear one large tooth, three smaller teeth, and are covered in part by a hood (Fig. 3). Just anterior to the anal funnel (Fig. 4) at the posterior end of the animal, the hooded hooks in the notopodium are replaced by simple acicular spines (Fig. 5). The first appearance of these spines ranges from the sixth to the second segment from the anal funnel. The acicular spines of the two notopodia of a segment shift towards the median line with each succeeding segment so that the spines of either side at the segment just anterior to the anal funnel nearly touch one another. This approaches the condition of a single dorsal line of acicular spines at this segment in *S. djiboutiensis* (Gravier, 1904, 1906).

The anal funnel (Fig. 4) is composed of six groups of acicular spines (Fig. 6) on each side. The number of spines varies dorsoventrally, right and left, and from specimen to specimen. Typically there are 3, 3, 2, 2, 1, 1 (dorsal to ventral) acicular spines on each side. However, the following variations were observed: for the left side 4, 4, 4, 2, 2, 2, and 4, 3, 2, 2, 1, 1; for the right side 4, 4, 2, 2, 2, 2, and 4, 4, 2, 2, 1, 1.

DISCUSSION

Scyphoproctus oculatus differs from the other two species in the genus by the possession of a pair of eyes on the prostomium and by only six groups of acicular spines on each side of the anal funnel. The prostomium of *S. djibou-*

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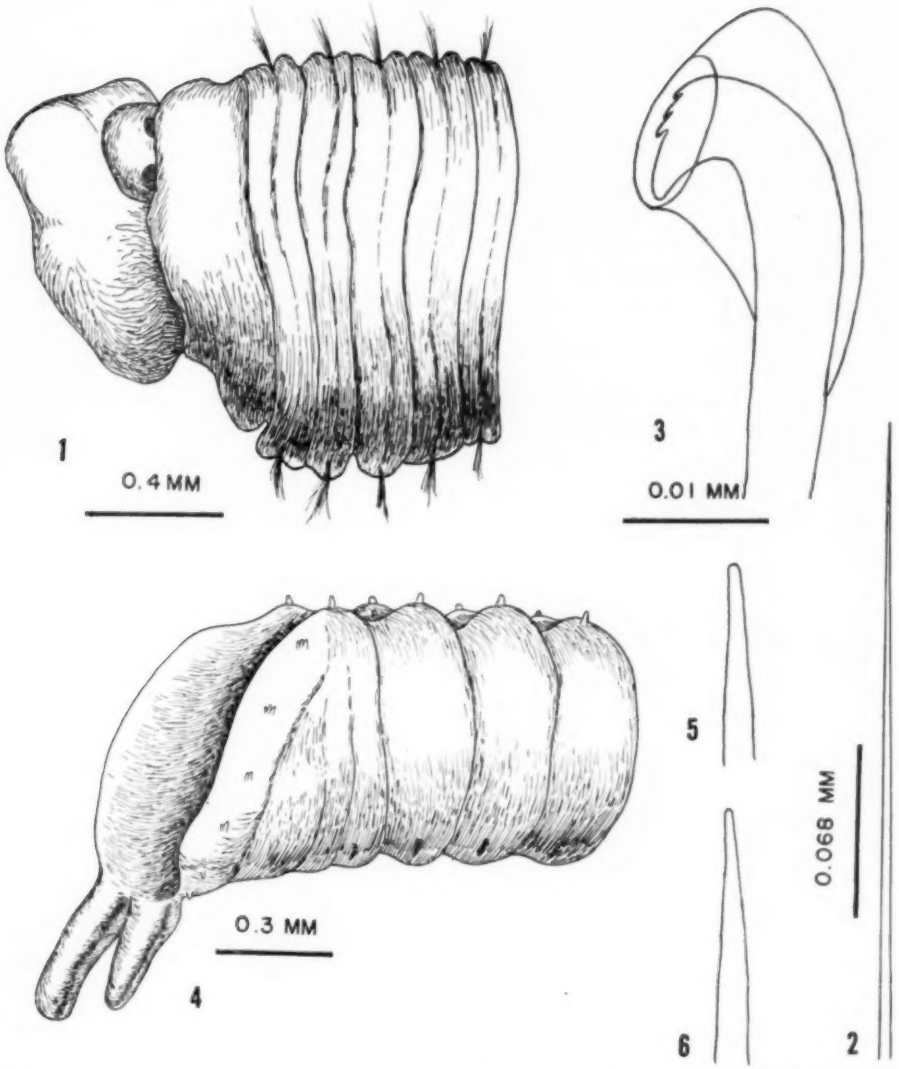
[2] Department of Biology and the Allan Hancock Foundation, University of Southern California, Los Angeles.



FIGS. 1–6. *Scyphoproctus oculatus* n. sp. 1, Anterior end in lateral view; left to right, everted proboscis, prostomium with both eyes shown, peristomium, setigerous segments 1 to 5 bearing capillary setae. 2, Capillary seta from segment 7. 3, Hooded hook from segment 15. 4, Posterior end in lateral view; left to right, anal funnel bearing two anal cirri and six groups of acicular spines and the posterior setigerous segments with acicular spines in the notopodium and hooded hooks in the neuropodium. 5, Acicular spine from a posterior notopodium; magnification as 2. 6, Acicular spine from anal funnel; magnification as 2.

tiensis lacks eyes, and the anterior end is unknown in *S. gravieri*. Both *S. djiboutiensis* and *S. gravieri* are characterized by having 11 groups of acicular spines on either side of the anal funnel. The number of spines is 4, 4, 3, 3, 3, 2, 2, 2, 1, 1, 1 in the former, and 13 (or 12), 7, 5, 5 (or 4), 4, 3, 2 (or 3), 2, 2, 2, 1 in the latter species.

Type Material

The holotype, seven paratypes, and additional specimens have been deposited in the polychaete collections of the Allan Hancock Foundation, University of Southern California.

Type Locality

Bottom of Newport Bay near the Pacific Coast Highway (Alternate 101) Bridge. The substrate consisted of sand and shell fragments at these stations.

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Evapotranspiration in Hong Kong: A Second Report[1]

C. S. RAMAGE[2]

THE FIRST REPORT on evapotranspiration in Hong Kong (Ramage, 1953)[3] describes installation of an evapotranspirometer battery, twenty months' measurement of potential evapotranspiration (P.E.) from grass surfaces, and comparisons of P.E. from grass and some common vegetables.

Comparison of measured P.E. with that computed from Thornthwaite's (1948) formula reveals that the formula when applied in Hong Kong gives values consistently low in winter and high in summer.

This leads to two possible conclusions:

1) The site of the evapotranspirometers is not representative of the area.
2) Thornthwaite's formula is not valid for Hong Kong.

The present paper will summarise the first five years' P.E. measurements at Hong Kong (October 1951 through September 1956), present arguments on the two possibilities mentioned above, discuss Penman's (1948) transpiration formula, and, finally, describe the derivation of a simple P.E. formula for Hong Kong.

FIVE YEARS' POTENTIAL EVAPOTRANSPIRATION MEASUREMENTS

Table I shows monthly totals of P.E. measured for three grass-covered soil tanks at the King's Park Radiosonde Station (22°19′N., 114°10′E., 213 feet above mean sea level) together with relevant meteorological data. Each tank has an internal area of four square meters. To save material, the central tank has a wall in common with each of the others. The site was unchanged throughout the period and there were no variations in methods of watering or of measuring rainfall and overflow. Except when one or two tanks were used briefly for growing vegetables, the results are means derived from all three tanks in the battery. Readings varied insignificantly and randomly between tanks, indicating a satisfactory local exposure and unlikelihood of leaks. In wet weather the overflow tanks occasionally flooded. Resulting errors have been eliminated from the final values.

POTENTIAL EVAPOTRANSPIRATION OF VEGETABLES

Validity of P.E. relative to grass for tomatoes, Chinese cabbage, and lettuce determined during the 1952 winter (table 1 of first report) was tested in the winter of 1953–54. The results appear in Table 2. It can be seen that ratios of vegetable P.E. to grass P.E. varied little from one winter to the next. The method of comparison thus appears to give results of real value to irrigation planners.

[1] Contribution No. 7 of Hawaii Institute of Geophysics. Scientific Report No. 1 of Contract No. AF 19 (604)-1942. The research in this document habeen sponsored in part by the Air Force Cambridge Research Center, Air Research and Development Command, under Contract No. AF 19 (604)-1942. Presented at the Ninth Pacific Science Congress, Bangkok, November, 1957. Manuscript received September 19, 1957.

[2] Meteorology Division, Hawaii Institute of Geophysics, University of Hawaii.

[3] This report also appeared on pages 112–124 of Johns Hopkins University Laboratory of Climatology, Publications in Climatology Vol. VII, No. 1, edited by J. R. Mather. (Contracts AF19 (604)-193, AF 19 (604)-289.)

TABLE 1
MONTHLY POTENTIAL EVAPOTRANSPIRATION AND METEOROLOGICAL OBSERVATIONS MADE AT KING'S PARK (22°19′N., 114°10′E., 213 FT. ABOVE M.S.L.) AND AT ROYAL OBSERVATORY (22°18′N., 114°10′E., 109 FT. ABOVE M.S.L.) FOR THE FIVE-YEAR PERIOD, OCTOBER 1951–SEPTEMBER 1956, AND ALSO FOR OCTOBER 1956–DECEMBER 1956

	YEAR	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.
Potential evapotranspiration (King's Park) mm.	1951										144	100	91
	1952	74	79	80	88	120	95	113	104	81	139	100	76
	1953	72	49	73	72	99	130	133	100	119	122	93	81
	1954	72	77	88	80	140	102	148	147	161	133	136	83
	1955	79	81	106	107	110	116	118	101	125	147	121	87
	1956	64	84	95	131	142	157	157	124	140	141	116	78
	5-YEAR MEAN	72	74	88	96	122	120	134	115	125	137	110	84
Rainfall (King's Park) mm.	1951										104	75	15
	1952	26	32	40	183	184	560	189	376	838	17	9	24
	1953	27	64	135	95	354	407	138	374	564	48	41	76
	1954	53	30	58	160	89	207	147	294	171	20	133	0
	1955	2	0	61	162	446	322	546	580	115	11	49	18
	1956	67	80	7	79	299	367	170	455	165	37	34	7
	5-Year Mean	35	41	60	136	274	373	238	416	371	40	61	27
Mean temperature (King's Park) °F.	1951										77	70	64
	1952	62	61	65	72	80	82	83	81	80	77	73	61
	1953	61	61	65	66	76	82	83	83	80	79	71	64
	1954	63	61	61	71	80	82	83	83	81	76	70	61
	1955	57	64	69	72	79	81	82	82	83	77	68	66
	1956	58	61	66	75	79	83	84	82	83	77	68	62

REPRESENTATIVENESS OF THE KING'S PARK SITE

An oil-drum evapotranspirometer (see Garnier, 1954) was installed at Kai Tak Airport (22°20′N., 114°12′E., 12 feet above mean sea level)and readings began in September, 1954. The tank was turfed with and surrounded by grass clipped to 1–2 inches and was watered from above. The site being in an extensive flat area near sea level differs considerably from King's Park where the evapotranspirometer is atop a small isolated hill.

Figure 1 shows results of the first year's simultaneous readings. For this period it is safe to assume that the oil drum did not develop leaks. At Kai Tak, in moisture deficient

TABLE 1, *continued*

MONTHLY POTENTIAL EVAPOTRANSPIRATION AND METEOROLOGICAL OBSERVATIONS MADE AT KING'S PARK (22°19'N., 114°10'E., 213 FT. ABOVE M.S.L.) AND AT ROYAL OBSERVATORY (22°18'N., 114°10'E., 109 FT. ABOVE M.S.L.) FOR THE FIVE-YEAR PERIOD, OCTOBER 1951–SEPTEMBER 1956, AND ALSO FOR OCTOBER 1956–DECEMBER 1956

	YEAR	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEPT.	OCT.	NOV.	DEC.
	5-Year Mean	60	62	65	71	79	82	83	82	81	77	70	63
Mean dew point temperature (Royal Observatory) °F.	1951										68	61	50
	1952	52	55	61	68	75	77	77	77	75	68	62	47
	1953	51	56	60	60	71	77	77	78	74	73	61	55
	1954	57	54	53	67	74	77	77	77	73	65	59	48
	1955	41	53	62	64	72	75	77	76	76	64	53	53
	1956	46	55	59	67	73	76	77	76	72	65	52	51
	5-Year Mean	49	55	59	65	73	76	77	77	74	68	59	51
Sunshine duration (Royal Observatory) hours	1951										197	135	189
	1952	168	78	84	114	196	152	192	177	165	240	264	138
	1953	130	59	75	61	125	194	275	241	114	211	141	153
	1954	160	116	109	69	221	159	254	206	218	256	213	150
	1955	210	147	121	174	169	137	160	208	253	289	181	229
	1956	165	66	102	175	137	214	263	229	229	242	172	164
	5-Year Mean	167	93	98	119	170	171	229	212	196	239	187	172
Mean wind speed (Royal Observatory) knots	1951										9.5	10.9	9.9
	1952	9.6	11.7	13.2	10.8	8.9	8.1	8.1	7.0	9.0	9.8	7.5	8.4
	1953	10.2	11.5	10.9	11.3	9.5	8.8	6.4	5.7	10.3	9.5	8.3	9.4
	1954	9.3	9.4	9.1	11.0	6.7	7.7	5.9	7.3	10.5	8.8	10.6	9.3
	1955	9.4	11.6	11.1	9.3	8.0	9.1	6.8	4.7	6.5	11.2	11.6	10.8
	1956	9.3	12.1	12.5	10.4	9.5	8.2	6.6	9.6	9.1	9.9	9.4	7.8
	5-Year Mean	9.6	11.3	11.4	10.6	8.5	8.4	6.8	6.9	9.1	9.8	9.8	9.6

months, grass surrounding the tanks could not be watered, while some flooding possibly occurred in moisture-surplus months. Since King's Park is not subject to these mensural drawbacks they may account for some of the differences between the two curves. It seems reasonable then to conclude that the King's Park site is probably a representative one.

TABLE 2
COMPARISON OF POTENTIAL EVAPOTRANSPIRATION FROM VEGETABLES AND GRASS

CROP	TOMATOES	CHINESE CABBAGE	LETTUCE
Planting date	28 Oct. 1953	28 Oct. 1953	2 Jan. 1954
Days to reach maturity	128 (last fruit)	61	79
Total crop weight (lbs.)	85 (poor crop)	34½	
(1) Total P.E. (mm.)	838	282	271
Average daily P.E. (mm.)	6.5	4.6	3.4
(2) Total P.E. of grass in same period (mm.)	354	182	193
Average daily P.E. of grass in same period	2.8	3.0	2.4
Ratio (1)/(2)	2.4	1.5	1.4
Mean temperature during period (°F.)	65	68	62
Ratio (1)/(2) for 1952 winter	2.3	1.6	1.7

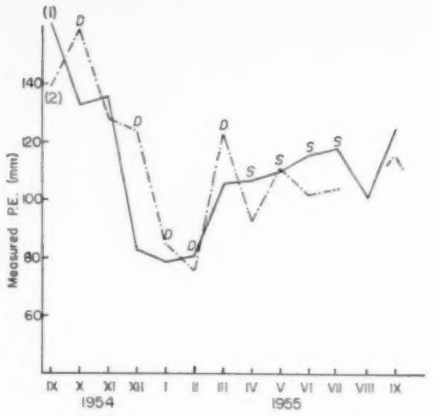

FIG. 1. Monthly potential evapotranspiration measured at King's Park (1), and at Kai Tak Airport (2). September 1954 through September 1955. "D" signifies that P.E. exceeded rainfall by at least 75 per cent and the letter "S" that rainfall was in excess by at least 35 per cent.

COMPARISON OF MEASURED POTENTIAL EVAPOTRANSPIRATION WITH VALUES DERIVED FROM THORNTHWAITE'S AND PENMAN'S FORMULAE

Thornthwaite's Formula

The conclusions of the first report are amply confirmed by the longer period of record. Figure 2 shows monthly means of P.E. derived from the five years' measurements. Again calculated values are too low in the dry winter and too high in the wet summer. Since investigators in Australia (Leeper, 1950), Nigeria (Garnier, 1954), and Trinidad (Smith, 1954) report similar shortcomings in the formula one must conclude that it should not be assumed to be valid for any monsoon or tropical maritime region.

Penman's Formula

Penman (1948, 1950), using energy conceptions, derives the following formula for estimating potential transpiration from vegetated areas. (It checks well with observations made in America and Europe.)

$$E_T = E_o \times f = f\,(\triangle H + 0.27E_a)\,/\,(\triangle + 0.27)\ \text{mm/day.}$$

Where E_T = potential transpiration

E_o = the hypothetical evaporation that would take place from an extended sheet of open water exposed to the weather conditions found over the site.

f, an empirically determined seasonal factor converting E_o to E_T, has the following values:

Nov. through Feb.	0.6
Mar., Apr., Sept., Oct.	0.7
May through Aug.	0.8

$\triangle$ = slope of vapor-pressure curve for water at mean air temperature T_a (mm mercury/°F)

$$H = R_A\,(1-r)\,(0.18+0.55n/N) - \sigma T_a^4 (0.56 - 0.092\sqrt{e_d})\,/\,(0.10+0.90n/N)$$

0.27 = the constant of the standard hygrometer equation (mm/°F)

$$E_a = 0.35\,(e_a - e_d)\,(1+u_2 \times 10^{-2})\ \text{mm/day}$$

R_A = theoretically calculable amount of radiation that would reach the earth in the

absence of an atmosphere, converted to an evaporation equivalent by putting 59 cal/cm² = 1 mm. evaporation.

r = reflection coefficient, to be taken as 0.05. For standard evaporation tanks with light walls and clean water it may be very much greater.

n/N = actual/possible hours of sunshine. In the first term in H it is a factor limiting incoming short-wave radiation; in the second it is a transform of a cloudiness factor limiting outward long-wave radiation.

σT_a^4 = theoretical black-body radiation at mean air temperature T_a; this too is in evaporation units like R_A.

e_d = saturation vapor pressure at dewpoint (mm Hg).

e_a = saturation vapor pressure at mean air temperature; hence $(e_a - e_d)$ is the mean saturation deficit.

u_2 = average wind speed in miles/day at 2 m. above the ground.

Since the formula incorporates both humidity and wind parameters it appeared likely to give more reasonable results than Thornthwaite's formula when applied in Hong Kong. The data listed in Table 1 have been used to calculate mean monthly P.E. according to Penman's formula and the values are plotted in Figure 2. They approach the observed values more closely than those determined by Thornthwaite's formula but err in the same sense, overestimating summer and underestimating winter P.E.

POTENTIAL EVAPOTRANSPIRATION FORMULA FOR HONG KONG

Deriving the Formula

In Penman's formula, the expression $E_a = 0.35\ (e_a - e_d)\ (1 + u_2 \times 10^{-2})$ mm/day incorporates humidity and wind parameters.

Figure 3 shows a plot of both E_a and mean daily observed P.E. at Hong Kong derived from the monthly means for five years. From October through January and from February

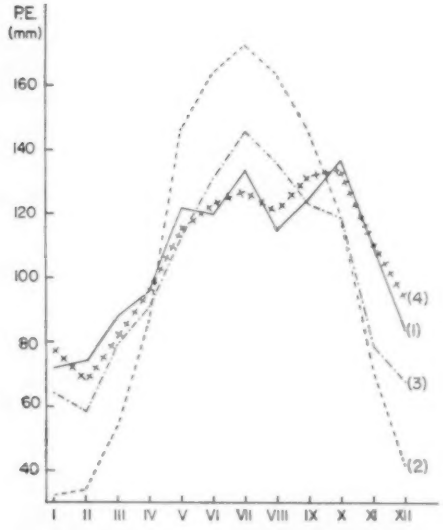

FIG. 2. Monthly means of potential evapotranspiration measured at King's Park (1), and calculated according to Thornthwaite's formula (2), Penman's formula (3), and the new formula (4). Based on five years' data.

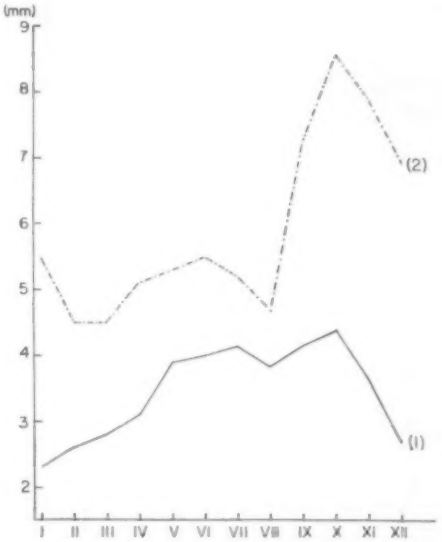

FIG. 3. Mean daily potential evapotranspiration measured at King's Park (1), and E_a (2). Based on five years' data.

TABLE 3
MEASURED AND CALCULATED MONTHLY POTENTIAL EVAPOTRANSPIRATION AT HONG KONG FOR 1953 AND OCTOBER THROUGH DECEMBER 1956 (MM.)

	1953												1956		
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Oct.	Nov.	Dec.
Measured	72	49	73	72	99	130	133	100	119	122	93	81	141	116	78
Thornthwaite formula	35	33	53	59	122	165	175	168	138	135	73	45	115	58	38
Difference	+37	+16	+20	+13	−23	−35	−42	−68	−19	−13	+20	+36	+26	+58	+40
Penman formula	64	46	65	76	106	140	160	144	114	104	69	59	125	85	57
Difference	+8	+3	+8	−4	−7	−10	−27	−44	+5	+18	+24	+22	+16	+31	+21
New formula	81	57	78	81	106	126	127	121	129	124	105	84	142	111	81
Difference	−9	−8	−5	−9	−7	+4	+6	−21	−10	−2	−12	−3	−1	+5	−3

through August the curves are similar although between these periods they undergo sharp relative displacements. Nevertheless, E_a seems to bear some intraseasonal relationship to measured P.E. This may explain why Penman's formula approximates Hong Kong observations more closely than does Thornthwaite's formula which does not explicitly embody humidity and wind parameters.

Thornthwaite attaches great importance to temperature in the evapotranspiration process. This was allowed for by combining e_a with E_a in the form $\sqrt{E_a} + \sqrt{e_a}$. When this expression is plotted against mean daily measured P.E. (Fig. 4), a good fit is provided by a straight line whose equation is

$$\text{P.E.} = \sqrt{E_a} + \sqrt{e_a} - 3.5 \text{ mm/day}$$

Values calculated from this equation and plotted in Figure 2 are in reasonable agreement with mean monthly measured P.E.

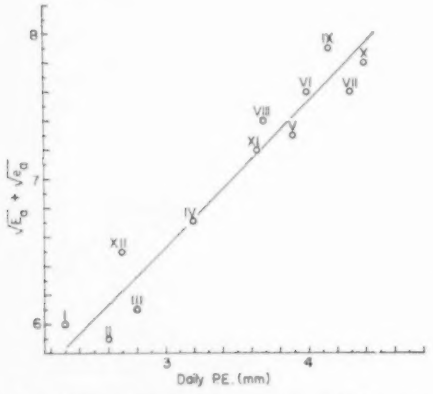

FIG. 4. Mean daily potential evapotranspiration measured at King's Park plotted against $\sqrt{E_a} + \sqrt{e_a}$. Based on five years' data.

Testing the Formula

1953 was the most abnormal year of the five-year period. Table 3 and Figure 5 depict

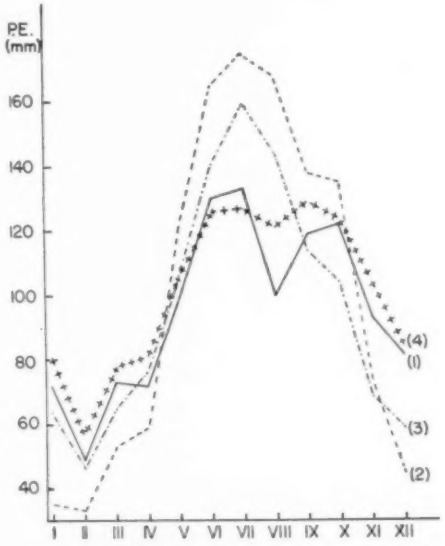

FIG. 5. Monthly potential evapotranspiration for 1953 measured at King's Park (1), and calculated according to Thornthwaite's formula (2), Penman's formula (3), and the new formula (4).

measured P.E. and P.E. calculated by the Thornthwaite, Penman, and new formulae. In addition, Table 3 compares the formulae for the three months following the five-year period. Again the new formula best approximates Hong Kong measurements.

CONCLUSIONS

Evapotranspiration formulae based on mid-latitude data should not be uncritically used in estimating P.E. for monsoonal or tropical maritime regions.

In such regions, humidity and wind may be as important parameters as temperature, and simple formulae similar to that derived for Hong Kong might fairly be used to calculate potential evapotranspiration.

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The Flora of Namonuito and the Hall Islands

BENJAMIN C. STONE[1]

APPROXIMATELY 160 miles northwest of Truk, in the Caroline Islands, lies Namonuito Atoll, straddling the 150th W. meridian. Lying successively to the east are Fayu, Nomwin, and Murilo atolls, comprising the Hall Islands. Together these strips of land amount to no more than a few square miles, but they are scattered over three and a half degrees of latitude, approximately eight and a half degrees north of the equator. Namonuito consists of some seven major islets and several minor ones. Beginning at the southwest, these are: Ulul (or Olol), Namonuito, Magererik (Magurchuk), Magur (Magerlap), Ono, Onari, Weltot, and Pisarach. Sixty miles east is Fayu, an uninhabited island which is visited from time to time because of the abundant fish and turtles. Thirty miles farther east is Nomwin Atoll, with its two inhabited islets, Nomwin and Fananu, and other smaller islets. East again of Nomwin is Murilo Atoll, of which Ruo and Murilo islets are inhabited. These major islets are strips of coralline land, rising to a height of 5 feet or rarely somewhat more, usually with a central depression.

The general aspect of any one of these islets is much like any other; a reef, a strip of beach, and the coconut-palm skyline. Granted the sparse flora and the omnipresent coralline soils, they have rather considerable variation. The three atolls here considered differed not only among themselves but also as a group differ from other atoll groups, such as the Marshall and the Gilbert islands. There are important differences in the floristic make-up and, consequently, in the ecological balance of the species present. Yet in a broader sense there is a remarkable sameness about the forested atolls of the Pacific, and many of the species herein recorded might reasonably be expected to occur on any of the Micronesian, or even Polynesian, atolls. This applies not only to indigenous species but to weeds and crop plants.

Namonuito, Nomwin, and Murilo were visited by the author in June and July of 1957 while collecting *Pandanus* specimens for Dr. Harold St. John's National Science Foundation Project, which was begun at the University of Hawaii in 1955.

These atolls have a fairly constant temperature usually ranging from 75° to 90° F.; breezes are nearly always present; rainfall, though scattered, supports a thriving forest flora in the less disturbed islets. Extreme dryness, such as may be encountered in the northern Marshall Islands, is not a feature of this area, though droughts may occur. The heat is most extreme on sandy spits with little or no plant cover, situations which are unfavorable to many species but which may be colonized by *Ipomoea pes-caprae*, *Scaevola frutescens*, *Fimbristylis atollensis*, and *Lepturus repens*.

Several of the islets have swampy central depressions, and on Pisarach there is a true swamp at the southern end with characteristic swamp species including *Acrostichum aureum*, *Cyclosorus goggilodus*, and *Bruguiera conjugata*. On certain islets, ordinarily uninhabited, a rather well-developed *Pisonia* forest flourishes, usually in company or codominant with *Eugenia*. The trees are large-boled and may rise to 70 or 80 feet. The undisturbed forests have little or no ground cover beneath the trees. These presumably native forests are now much cut-over and cleared, or burned for clearings. In these clearings a wide array of species, both native and weedy, occurs; near villages various crop plants are cultivated, namely, coconut palms, taros, bananas, papayas, and tobacco. Other large trees fre-

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quently found are *Calophyllum Inophyllum*, *Ficus tinctoria*, *Barringtonia asiatica*, and *Ochrosia oppositifolia*, which are noticeable along the beaches behind the front ranks of *Scaevola* and *Messerschmidia*. *Ochrosia* tends to form pure stands here and there, and in such places its seedlings are very numerous. Besides these tree species, and a few others, most of the vegetation is of shrubs, rising to 15 or 25 feet on occasion, and of vines, herbs, and crop plants. Needless to say, the flora is not a rich one. There are 94 species recorded here, of which about 52 can be reasonably construed as indigenous; of the remaining 42 species, 22 are clearly introduced food or ornamental plants; the remaining 20 species are presumably accidental introductions and weeds.

Nevertheless there is some diversity in the vegetation; islets differ from one another, and each islet consists of two or more zones. The indigenous ecological zones probably consisted of the following:

(1) The strand forest, the outermost line of vegetation on the beaches, consisting of *Scaevola*, *Messerschmidia*, *Morinda*, and *Guettarda* as the usual dominants, with *Ochrosia*, *Terminalia*, *Pandanus*, *Cordia*, *Allophylus*, and *Hernandia* occurring locally as individuals or sometimes in small stands. Less frequent members of the strand association are *Suriana* and *Sophora*. Several creeping or scandent vines are present, chiefly *Ipomoea pes-caprae*, *I. gracilis*, *Vigna*, *Canavalia*, *Triumfetta*, and the parasitic *Cassytha*. *Wedelia* is a scandent or rarely erect shrub of both exposed and shady areas. The grass *Lepturus* and the sedge *Fimbristylis* are both very common, but tend to occur most abundantly in a savannah-like subassociation of windswept narrow extremities, often in company with stunted, scattered shrubs, especially *Pandanus*.

(2) *Pisonia* forest. Before the coming of the Micronesian inhabitants, it seems possible that many, if not all, of the islets may have had dense pure stands of *Pisonia grandis*, the viscid fruits of which are spread by birds. Some remnants of these stands remain on Megererik, Magur, and according to another observer, on Fayu. As noted by the author, the *Pisonia* forest on Magur was not a pure stand, but contained many large trees of *Eugenia javanica*. This is perhaps the result of deliberate cultivation or at any rate a long-term result of such cultivation. *Eugenia* is not known from the Marshall Islands and seems not to be present on any of the Caroline Islands atolls in the vicinity of Ponape (such as Mokiel, Pingelap, Ngatik, Nukuoro, and Kapingamarangi).

(3) Intermediate forest. This comprises an area variable in extent, sometimes lacking, sometimes replacing the *Pisonia* forest. It is actually not a homogeneous association but consists of varying proportions of the smaller trees, either in stands or mixed, including *Ochrosia* (usually in pure stands), *Pipturus*, *Allophylus*, *Pandanus*, *Barringtonia* (which may also be in the open strand), *Calophyllum* (more usually along the strand), and occasionally *Hibiscus tiliaceus*.

(4) Coconut and breadfruit forests. These dominate most of the central areas of the islets and are the result (at least originally) of deliberate planting. The seeded breadfruit varieties replenish the forest quickly and naturally, and there are on some islets almost pure stands of breadfruit trees. Often they will be accompanied by *Ficus*, *Eugenia*, and *Crataeva*. The coconut groves may be open, with a sparse ground cover, or choked with shrubs. On Pisarach many coconuts grow in a sub-swampy area.

(5) Swamps, both artificial and natural, occur in several islets. The artificial swamps are pits planted with *Cyrtosperma* or *Colocasia*. On Pisarach Islet the naturally swampy southern end is partially utilized for taro cultivation. A few trees of *Bruguiera conjugata* occur here, characterized by white calyces rather than the usual glossy red calyces, and herein described as forma *alba*. Other swamp species include the ferns *Acrostichum aureum* and *Cyclosorus goggilodus*, and the small sedge *Eleocharis geniculata*.

The intertidal zone, whether of calm, sandy-bottom lagoons or of coral pavement or boulders, is a very important ecological feature of an atoll, but except for the ubiquitous marine angiosperm *Thalassia*, which was noted at Nomwin Atoll, the vegetation is of algae and is not cataloged here.

Collections were made on Ulul (June 22, 1957), Magur (June 29), Ono (June 30), and Pisarach (July 2) islets of Namonuito Atoll; on Nomwin (July 3) and Fananu (July 4) islets of Nomwin Atoll; and on Ruo Islet (July 5) of Murilo Atoll. The specimens have been deposited in the herbarium of the Bernice P. Bishop Museum, Honolulu, Hawaii.

Economy

The island economy is completely agricultural. The coconut furnishes, in the form of copra exports, the principal or only source of income, as well as a wide array of uses for food, shelter, and cordage. Wherever possible, coconut palms have been planted and the original forests replaced. In Namonuito Atoll, on Magererik and Magur islets, there are some stands of *Pisonia* forest in relatively undisturbed condition, however. These are usually intermixed with breadfruit and *Eugenia* trees. Breadfruits are one of the staple foods; the tubers of *Cyrtosperma*, and to a lesser degree, of *Colocasia*, are the other staples. Breadfruits are preserved for future use in shallow depressions in the earth which are lined with banana leaves and covered with stones. In this manner they are kept several months as a reserve to be used in the months during which the breadfruit trees bear no fruit. Breadfruit seeds furnish a minor but well-liked source of food. *Alocasia*, the third "taro," is not actively cultivated, but grows spontaneously and is used on occasion for food, especially during droughts or famines. *Tacca* is a similar reserve food. Papayas, bananas, pumpkins, sweet potatoes, and pandanus fill out the vegetable diet. Chickens, pigs, and seafood are the main sources of meat. Much of the income derived from the sale of copra is spent for imported foods, such as rice, flour, sugar, coffee, and tinned meats, as well as for clothing, hardware, and tobacco. Most islets also have some plants of *Nicotiana* to furnish tobacco between visits of the copra steamer.

Brief Description of the Islets

The islet of Ulul, or as it is sometimes spelled, Olol, is dominated by coconut palms. Other trees include breadfruits, *Pandanus*, *Ficus*, *Eugenia*, *Hernandia*, *Barringtonia*, *Hibiscus*, *Allophylus*, *Premna*, *Calophyllum*, and *Casuarina*. Abundant shrubs are *Scaevola*, *Messerschmidia*, *Callicarpa*, *Pipturus*, and *Clerodendrum*. *Glochidion* and *Wedelia* are also rather frequent. The low herbaceous species include *Oplismenus*, *Thuarea*, *Fimbristylis*, *Microsorium*, *Nephrolepis*, *Portulaca*, *Ipomoea*, and *Triumfetta;* climbing and creeping vines include the very abundant *Piper fragile?* and *Piper ponapense*, *Vigna*, *Canavalia*, and *Cassytha*. Introduced weeds include *Eleusine*, *Chrysopogon*, *Cenchrus*, all grasses, and *Euphorbia hirta*, *E. thymifolia*, and *Vernonia*. In the village, *Plumeria*, *Nerium*, *Crinum*, *Hibiscus rosa-sinensis*, *Mirabilis*, and *Zephyranthes* are cultivated as ornamentals. Characteristic of Ulul and the greater part of Namonuito Atoll is the great abundance of *Piper* vines in the forest, forming a ground cover and climbing high up tree trunks. *Glochidion*, however, is infrequent here, and is not nearly so important a component of the under-story as it is on Nomwin Islet.

On Magur Islet, there is a good stand of forest, consisting of *Pisonia*, *Eugenia*, and breadfruits. The second story of this forest, developed especially at the forest fringes, consists of *Morinda*, *Allophylus*, *Crataeva*, *Ficus*, papayas, and seedlings of the upper-story trees. The ground cover is chiefly *Piper fragile?*, *Nephrolepis*, *Microsorium*, *Wedelia*, and *Vigna*. *Asplenium nidus* is an abundant epiphyte and is also sometimes terrestrial. The soil developed here is a light black organic mulch mixed with white coral sand and coral

fragments. In depth this soil may reach six inches, a fairly good soil for an atoll.

Ono Islet consists chiefly of coconut groves and the usual strand species. *Pisonia* is absent, and so, apparently, is *Glochidion*.

Pisarach Islet has both the largest village (over 100 people) and the most varied vegetation. Although no *Pisonia* forest was seen, the abundant large breadfruit trees, mixed with *Eugenia*, *Ficus*, *Ochrosia*, *Crataeva*, and coconut palms make up a tall shady forest with a sparse under-story over much of the islet. The southern end of the islet is a natural swamp. Irrigation channels crisscross part of it, and *Cyrtosperma*, *Colocasia*, and bananas are planted. Most of the swamp is, however, a tangled mass of small trees, clambering vines, and clumps of marsh fern, all rooted in mud or standing pools. The seaward margin of the area is sandy, and behind this is a line of coral fragments, which quickly merges into the inner area of black, sandy, then mucky soil. Coconuts grow here to some extent. Trees of the swamp are *Hibiscus tiliaceus*, *Barringtonia*, *Premna*, *Pandanus*, *Eugenia*, and *Bruguiera*. In the cultivated portions, besides the taros, there are *Eleocharis*, *Cyclosorus*, *Cyperus*, *Jussiaea*, *Vigna*, *Clerodendrum*, and *Digitaria*. Forming thickets or clumps, often over large areas, is *Acrostichum*, and *Vigna* and *Clerodendrum* scramble over the other species. In the muddy but not water-covered areas coconut palms, breadfruits, *Ficus*, *Eugenia*, and *Crataeva* are found, with *Nephrolepis*, *Microsorium*, *Piper*, *Thuarea*, and *Digitaria* as ground cover.

Nomwin Atoll is notable for the abundance of *Glochidion*, which is the dominant shrub in the forest under-story. It accounts for at least fifty per cent of the ground cover on Nomwin Islet. The eastern extremity of Nomwin Islet, however, is a wind-swept savannah dominated by dwarf stunted pandanus and the rosette-forming *Fimbristylis atollensis*. The usual strand shrubs occur only as severely stunted individuals. The weedy *Eragrostis amabilis* is abundant here also, complete flowering specimens of which may measure only one inch in length. The soil is a rough mass of coral fragments slightly intermixed with fine sand, and no organic layer except fallen pandanus leaves.

Murilo Atoll is very similar to Nomwin, being dryish, with no swamps, the soil light, thin, and sandy. The islet profile shows a considerable central dip, the seaward rim being built up of coral boulders forming a "cliff" some eight feet in height, sloping steeply to a narrow sandy beach fronted by a reef of coral pavement. The forest is chiefly coconut palms, breadfruits, *Eugenia*, *Pandanus*, *Crataeva*, and the strand trees. The forest under-story is mainly *Wedelia*, both species of *Piper*, *Callicarpa*, *Vigna*, *Morinda*, and *Ipomoea gracilis*. *Glochidion* is conspicuously absent. The lagoon shore is dry, wind-swept, and open; it is notable for the presence of *Suriana*, *Sophora*, and *Euphorbia Chamissonis*, all in great abundance, as well as the usual strand species.

As can be seen from the brief summaries above, the floristic composition and the ecological patterns of the various islets differ to a surprising extent. The abundance of *Piper* on many islets, and the abundance of *Glochidion*, on Nomwin especially, though also to a lesser extent on Ulul, is in marked distinction from atolls in the Marshall Islands, or from Mokiel, Pingelap, Ngatik, Nukuoro, or Kapingamarangi. Curiously, the reef islets of Truk, like Nomwin, abound in *Glochidion;* but on most of Namonuito and Murilo it is apparently absent. On the high islands of Truk is a large shrub, abundant on low hillsides, which is probably *Glochidion ramiflorum* Forst. Whether the atoll *Glochidion* is conspecific is a matter of doubt, and until a monographic treatment appears, there seems little value in appending one of the dubious names to these plants. As Croizat (1943) shows, the delimitation of species in the genus is still highly problematic. Another plant quite common on both the high and low islands of Truk, but which apparently does not occur at all in Namonuito or the Hall Islands, is *Polyscias grandifolia*.

Vernacular Names

The people of the Namonuito and Hall islands are culturally and linguistically close to the Trukese. The plant names recorded here are frequently identical with, or at least similar to, the Trukese names; but variations in pronunciation, especially in certain characteristic consonant changes, will be frequently noted. The spelling used here is only an approach to the actual pronunciation, but should be understandable if the following rules are followed: the vowels are pronounced as in Spanish, except that à is the short sound, as in the English "fat"; ö, with the umlaut, is equivalent to the German sound of ö or oe; the r is rolled; j, ch, and sh are more or less equivalent and interchangeable sounds, depending on locale and other factors; k and g are similarly often interchangeable; and the consonants l, n, and r, are very flexible, and interchange or supersede each other from area to area. A few differences in the spoken language between Namonuito, Nomwin, and Murilo occur, mostly in pronunciation, and even between different islets of Namonuito Atoll (which may be out of sight of each other, over the horizon). For example, the edible pandanus variety called "kenlau" in Ulul is "kinlau," "killau," "kirau," or "genlau" in other islets; and on Truk it may be called "killau," "sillau," or even "sinnau." It must be cautioned that the names given are very local. For further information on the Trukese language, consult Samuel H. Elbert's *Trukese-English Dictionary* published by the U. S. Naval Military Government.

Check-list

The catalog of the flora is brief and includes no descriptions or full synonymies. However, a key is supplied to aid in the identification of species. Most of the plants are well known and widely distributed, but a few present problems of nomenclature or identification which are indicated.

The families are arranged according to Engler and Prantl merely for convenience. The original source of the species description or combination is given for each plant.

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KEY TO THE SPECIES

Though most of these plants are familiar to botanists, I have included this key for the use of anyone who may visit these islands. The key is of course highly artificial, and should not be used in other areas; it is not technical, and certain oversimplifications and omissions of more fundamental characters will be overlooked, I hope, in the interest of simplicity.

Group I. Ferns

Flowerless plants bearing spores usually as a brown powder in sporangia grouped in sori as round dots, long lines, or solid masses, on the backs of the fronds or pinnae

Fronds simple, up to several feet long, forming a large rosette; sori in long oblique lines . . . . . **Asplenium**

Fronds lobed or divided

Spores not grouped in sori, but covering the entire back of the fertile frond . . . . . **Acrostichum**
Spores grouped in sori, not covering the back of the frond
Fronds deeply parted, the segments entire . . . . . **Microsorium**
Fronds pinnate, the segments dentately or crenately lobed or parted
Segments crenately lobed; sori reniform; forest fern with fronds up to 4 ft. long . . . . . **Nephrolepis**
Segments dentately parted; sori round; swamp fern with fronds usually less than 2 ft. long . . . . . **Cyclosorus**

Group II. Flowering Plants

A. Trees or shrubs with woody stems (See also B and C)
Leaves minute, toothlike, borne at the joints of the needlelike, green, jointed stems which function as leaves; fruit a small woody cone . . . . . **Casuarina**
Not as above
Leaves 8–12 ft. long, pinnate; trunk unbranched . . . . . **Cocos**
Leaves not as above; trunk usually branched
Leaves 2–7 ft. long, spiny along the edges and along the midrib on the underside; fruit a head of green to orange woody drupes . . . . . **Pandanus**
Leaves and fruit not as above
Leaves lobed, parted, or divided into leaflets
Leaves lobed or parted, or subentire occasionally, but never divided into leaflets; sap milky
Leaves palmately-pinnately divided; trunk often unbranched; fruit pearshaped, fleshy, orange . . . . . **Carica**
Leaves pinnately lobed or parted, or occasionally subentire; fruit globose or elongate, green, of many carpels . . . . . **Artocarpus**
Leaves divided into leaflets
Leaves ternate, i. e., divided into 3 leaflets
Fruit red, globose, ¼–½ in. diameter; flowers minute, greenish, borne in spikes . . . . . **Allophylus**
Fruit brownish or greenish, flecked with white, 4–10 in. long; flowers large, with white or creamy stalked petals . . . . . **Crataeva**
Leaves divided into more than 3 leaflets
Flowers yellow and red; leaflets smooth, green . . . . . **Caesalpinia**
Flowers yellow; leaflets with white hairs . . . . . **Sophora**
Leaves simple, not at all divided or lobed, never compound
Sap milky or yellowish, viscid
Sap yellowish; secondary leaf-veins curving-parallel; fruit spherical, woody, 1 in. diameter . . . . . **Calophyllum**
Sap milky-white; leaf-veins reticulate
Flowers less than ⅛ in. long, hidden inside a globose, fruitlike organ
Leaves unequal at base; veins raised below; leaves up to 12 in. long . . . . . **Ficus tinctoria**
Leaves subequal at base; veins not conspicuously raised below; leaves 2–4 in. long . . . . . **Ficus ramentacea?**
Flowers larger than ⅛ in. long, borne externally, with evident petals, ¼–1½ in. long

Flowers white; petals linear, less than ½ in. long; fruits twinned . **Ochrosia**
Flowers red, yellow, or white, with broad petals
Leaves narrowly elliptic or lanceolate, dull green, 4–6 in. long; flowers red, pink, or white, solid color . . . **Nerium**
Leaves glossy, broader, elliptic to obovate, up to 1 ft. long; flowers red and yellow, yellow and white, or varicolored . . . **Plumeria**
Sap clear, watery
Stems and twigs thorny; small tree . . . **Citrus**
Stems and twigs thornless
Leaves cordate, more or less heart shaped
Scandent shrub; leaves opposite; flowers yellow, in heads . . . **Wedelia**
Erect shrubs or trees; leaves alternate or spiral
Flowers tubular, red or yellow; stamens joined in a column
Flowers red; village shrub . . . **Hibiscus rosa-sinensis**
Flowers yellow with a maroon eye . . . **H. tiliaceus**
Flowers and stamens not as above
Leaves with silvery hairs below; fruit a whitish fleshy berry . **Pipturus**
Leaves smooth, hairless; fruit a black nut set in a green cup . . . **Hernandia**
Leaves not cordate or heart shaped
Leaves narrow, elliptic to lanceolate, with tapering pointed tips
Scandent shrubs; leaves opposite; flowers tubular, white, with pink exserted stamens . . . **Clerodendrum**
Erect shrubs or trees; flowers not as above
Leaves opposite
Trees; leaves smooth, hairless; flowers white to cream . . . **Eugenia**
Shrubs; leaves with silver-green hairs below; flowers lavender or bluish . . . **Callicarpa**
Leaves alternate or spiral
Leaves varicolored red, green, and yellow . . . **Codiaeum**
Leaves green, not varicolored
Shrubs, leaves paper thin
Flowers yellow, not enclosed by bracts; sparsely branching weak shrub . . . **Jussiaea**
Flowers white, enclosed by conspicuous pink or magenta bracts; branching shrub . . . **Bougainvillea**
Trees; leaves thick to leathery . . . **Bruguiera**
Leaves broad, ovate or obovate, or if narrow the tip blunt to obtuse-angled
Leaves fleshy, lanceolate-obovate, 1–2 in. long; flowers yellow; twiggy shrub . . . **Suriana**
Not with the above combination of characters
Leaves markedly obovate
Flowers borne in spikes
Fruit red, ovoid, keeled, slightly flattened, 1-seeded, ca. 1 in. long . . . **Terminalia**
Fruit greenish-yellow, flat, with 2 horns, 2-seeded, ½–¾ in. long . . . **Soulamea**

Flowers borne singly or in panicles
Flowers borne in panicles
Leaves with white hairs; flowers borne in a scorpioid cyme . . . . . **Messerschmidia**
Leaves smooth green; flowers not borne in a scorpioid cyme
Flowers less than ½ in. long, bilabiate, bluish, borne in flat-topped corymbose panicles; stamens 4 . . . . . **Premna**
Flowers more than ½ in. long, white, regular, borne in loose panicles; stamens numerous . . . . . **Eugenia**
Flowers borne singly
Leaves opposite; flowers tubular, white, 4-petaled . **Guettarda**
Leaves alternate or spiral
Flowers tubular at base but split along the upper side, white; fruit a small white berry; leaves slightly fleshy . . . . . **Scaevola**
Flowers with separate white petals, numerous pink stamens, 3 in. across; fruit a large woody box; leaves thin with a reddish midrib . . . . . **Barringtonia**
Leaves round, ovate to elliptic, but not markedly obovate
Leaves round, concave, saucer-like . . . . . **Nothopanax**
Leaves not as above
Flowers tubular, red or orange . . . . . **Cordia**
Flowers never red or orange
Flowers borne in umbels; fruits narrow, sticky; large forest trees . . . . . **Pisonia**
Flowers borne otherwise; fruits not as above; shrubs
Fuits compound, white, fleshy, 1–2 in. long . . . . **Morinda**
Fruits flattened, greenish, dry, ¼–½ in. wide, with red wedge-shaped seeds . . . . . **Glochidion**

B. Herbs, sometimes very large, or vines (See also A and C)
Marine plants growing in salt water, with thin flat elongate leaves . . . . . **Thalassia**
Not marine plants
Leafless vines with greenish or orange stems, parasitic . . . . . **Cassytha**
Not leafless vines
Large herbs with auriculate leaves, growing from tubers
Leaves with rounded auricles
Leaves pale green or glaucous; plants seldom over 2 ft. tall in cultivation . . . . . **Colocasia**
Leaves glossy green; plants up to 10 ft. or more . . . . . **Alocasia**
Leaves with sharp-pointed auricles . . . . . **Cyrtosperma**
Leaves not auriculate; roots not tuberous (except *Tacca*)
Leaves palmately then pinnately divided; flowers bearing numerous long threadlike filaments . . . . . **Tacca**
Leaves and flowers not as above
Vines with climbing or creeping stems
Leaves ternate, of 3 leaflets

Flowers pink; pods flattened ..... **Canavalia**
Flowers yellow; pods cylindric ..... **Vigna**
Leaves not ternate
Leaves pinnately compound ..... **Derris**
Leaves simple or lobed, not compound
Leaves lobed
Leaves trilobate, hairy; fruit prickly; flowers yellow ..... **Triumfetta**
Leaves bilobate, smooth; fruit smooth; flowers pink ..... **Ipomoea pes-caprae**
Leaves not lobed
Leaves cordate
Leaves reddish or purplish ..... **Ipomoea batatas**
Leaves green
Flowers tubular, over 1 in. long
Flowers pink or purple ..... **Ipomoea gracilis**
Flowers yellow ..... **Cucurbita Pepo**
Flowers minute, less than ⅛ in. long, without petals, borne in spikes
Spikes 1 in. long, ¼ in. wide ..... **Piper fragile?**
Spikes 2–5 in. long, ⅛ in. wide ..... **Piper ponapense**
Leaves not cordate, glaucous below ..... **Piper ponapense**
Not vines; erect or low herbs
Large treelike herbs with entire leaves 3–6 ft. long; fruits in clusters, pendent, yellow, fleshy ..... **Musa**
Not treelike
Flowers 3-petaled, white; leaves oblong-lanceolate, in 2 ranks; roots with ginger odor ..... **Hedychium**
Not as above
Leaves elongate, forming rosettes, up to 3 ft. long
Flowers pink; plants usually less than a foot high ..... **Zephyranthes**
Flowers white; plants 2–5 ft. tall ..... **Crinum**
Leaves not elongate, not in rosettes
Sap milky
Flowers small, white
Leaves purplish; stems herbaceous
Leaves minute, less than ½ in. long, hairless; plants prostrate ..... **Euphorbia thymifolia**
Leaves larger, hairy; plants erect ..... **E. hirta**
Leaves green; stems sometimes woody at base ..... **E. Chamissonis**
Flowers red and yellow ..... **Asclepias**
Sap not milky
Flowers tubular, pink or purplish
Flowers borne in heads; small herbs ..... **Vernonia**
Flowers not in heads; shrubs or large herbs
Leaves hairy ..... **Nicotiana**
Leaves hairless ..... **Mirabilis**

Flowers yellow or white
Flowers borne in heads ..... **Synedrella**
Flowers not borne in heads
Leaves minute, less than ¼ in. long; plants prostrate, often on rocks ..... **Pilea**
Leaves larger; plants erect
Leaves fleshy, salty to taste, ½–1 in. long
Stems reddish; leaves obovate ..... **Portulaca** sp.
Stems green; leaves elliptic ..... **Portulaca samoensis**
Leaves thin, tasteless
Stems reddish; leaves toothed ..... **Fleurya**
Stems green; leaves entire
Flowers not tubular
Flowers down-pointing, borne in terminal spikes ..... **Achyranthes**
Flowers lateral, axillary ..... **Phyllanthus**
Flowers tubular, 4-petaled ..... **Hedyotis**

C. Grasses and sedges; flowers small, greenish or brownish; leaves narrow, elongate (See also A and B)
Stems triangular; inflorescence subtended by leaflike bracts ..... **Cyperus**
Stems round; inflorescence not bracteate
Rosette plants with solid stems
Inflorescence branching, borne on leafless scapes ..... **Fimbristylis**
Inflorescence a single subglobose head ..... **Eleocharis**
Not rosette plants, or if so, stems hollow
Fruit a spiny burr, borne in a spike ..... **Cenchrus**
Fruit not spiny
Inflorescence a narrow cylindric spike breaking at joints when old; plants sometimes rosette-forming ..... **Lepturus**
Inflorescence not jointed and disarticulating
Spikes digitate, 2 or more borne palmately
Spikelets with several florets ..... **Eleusine**
Spikelets with 1 floret
Spikes 3 or more, digitate; fruit cartilaginous-indurate, not rigid **Digitaria**
Spikes 2, conjugate; fruit indurate, rigid ..... **Paspalum**
Spikes not digitate
Giant grass with long silky panicles 1 ft. or more long; culms woody, often striped with purple ..... **Saccharum**
Not as above
Spikelets on one side of the rachis
Spikes several, distant ..... **Oplismenus**
Spikes 1 or 2, close, hidden ..... **Thuarea**
Spikelets on both sides of rachis
Spikelets in a diffuse panicle; panicle compound, greenish, the spikelets minute ..... **Eragrostis**
Spikelets in a stiff panicle which is simple, reddish ..... **Chrysopogon**

TAXONOMIC CHECK-LIST

PTEROPSIDA

Class *FILICINAE*

POLYPODIACEAE

Acrostichum aureum L., Sp. Pl. 1069, 1753.

NAMONUITO: Pisarach Islet, south end, abundant in swamps, July 2, 1957, Stone 2137. N.v. "apeu."

Asplenium nidus L., Sp. Pl. 1079, 1753.

NAMONUITO: Magur Islet, epiphytic, June 29, 1957, Stone 2121. Observed on most islets.

Cyclosorus goggilodus (Schkuhr) Link, Hort. berol. 2: 128, 1833.

NAMONUITO: Pisarach Islet, south end, in swamps and taro patches, July 2, 1957, Stone 2142.

Microsorium scolopendria (Burm. f.) Copeland, Calif. Univ., Pubs., Bot. 16:112, 1929.

NAMONUITO: Magur Islet, in *Pisonia-Eugenia* forest, terrestrial or with climbing rhizomes, June 29, 1957, Stone 2101. NOMWIN: Nomwin Islet, in forest west of village, common, July 3, 1957, Stone 2162. Observed on all islets. A highly variable fern, extremely narrow-segmented forms of which, without much taxonomic basis, have been distinguished as var. *longisecta* H. Ito ex Hosokawa. Since ecological conditions seem to account for dwarf, nonpinnate forms, for the varying thickness of the fronds in various conditions of exposure and moisture, and for absolute size, it seems probable that this variety also is so determined. Glassman (1952:49) places this variety in synonymy with the species. N.v. "tiji."

Nephrolepis biserrata (Sw.) Schott, Gen. Fil. t. 3, 1834.

NAMONUITO: Magur Islet, in *Pisonia-Eugenia* forest, frequent, June 29, 1957, Stone 2094. Observed on all islets. N.v. "amerei."

Class *ANGIOSPERMAE*

Subclass *MONOCOTYLEDONAE*

PANDANACEAE

Pandanus sp.

Thirty-eight specimens were collected in the three atolls, all of them of section *Pandanus* and representing a wide array of fruiting and flowering material. Heretofore usually construed as *P. tectorius* Sol. or *P. odoratissimus* L.f., the identity of these specimens must await the completion of current research. However, two readily recognizable edible varieties may be listed here: one, which has been named *P. cylindricus* Kanehira, bears a large, elongate, cylindric syncarp up to 45 cm. long, composed of flat-topped, smooth-sided, 15-carpellate phalanges. These are nearly always completely sterile, the seeds aborting, and as a result, little if any hard endocarp develops, and the phalanges, after weathering, may be pulled apart with one hand. The other varieties have a tough and almost unbreakable endocarp. This one is commonly called "kinlau," "killau," or "kinnau."

Another edible variety is "fàch-era," which has a large elliptic syncarp, and phalanges with 10–15 carpels; the middle area of each phalange is expanded, and the sides are creased and lined with corky scars. This variety is called "ajbwirik" in the Marshall Islands, where it is abundant. It has been found also in the Ponape district.

The general term for *Pandanus* is "fàch." A variety used only for its leaves, with a shrub habit and conspicuous reddish bark, is called "fàch-en-luta," and is said to be from Rota, in the Marianas. It is apparently sterile. "Fàch" is also the term for an individual phalange of the fruit; "umun" means syncarp or head; "chön" means leaf. "Fàch-en-wan," applied to all the "wild" forms, apparently means "forest pandan." Several of the wild forms are used, on occasion, for food, but "kinlau" and "fàch-era" are the really prized edible fruits.

Besides the coconut palm, the pandanus is perhaps the most useful plant, its leaves providing thatch for roofing and walls, and plaiting materials for mats, handbags, handi-

crafts, and, in ancient times, sails; the root fibers are useful for temporary cordage; and the fruits of certain varieties are a valuable food.

HYDROCHARITACEAE

Thalassia hemprichii (Ehrenb.) Aschers., in Engler and Prantl, Nat. Pflanzenfam. 2(1): 254, 1889.

NOMWIN: Nomwin, lagoon waters, observed.

GRAMINEAE

Chrysopogon aciculatus (Retz.) Trin., Fund. Agrost., 188, 1820.

NAMONUITO: Ulul Islet, observed in village. N.v. "fadil."

Cenchrus echinatus L., Sp. Pl. 1050, 1753.

NAMONUITO: Ulul Islet, observed. A weed on many islets.

Digitaria pruriens (Fisch. ex Trin.) Buse, Miq. Pl. Jungh. 379, 1854.

NAMONUITO: Magur Islet, in burned-over clearing, frequent, often diseased, June 29, 1957, Stone 2123. Observed on several islets.

Eragrostis amabilis (L.) Wight and Arnott ex Hook. and Arnott, Bot. Beechey Voy. 251, 1841.

NAMONUITO: Magur Islet, in village, June 29, 1957, Stone 2106. Observed on all islets. N.v. "namanaman."

Eleusine indica (L.) Gaertner, Fruct. et Seminif. Pl. 1: 8, 1788.

NAMONUITO: Ulul Islet, observed. Magur Islet, in village, June 29, 1957, Stone 2107. A common weed. N.v. "bukúr."

Lepturus repens (Forst.f.) R.Br., Prodr. 207, 1810.

NOMWIN: Nomwin Islet, along strand and in woods, July 5, 1957, Stone 2164. Observed on most islets. The shade forms are larger, more lax, not so markedly rosette forming, and seem to be var. *subulata* Fosberg; the plants found in exposed sandy beach areas tend to be smaller and to form rosettes, as in var. *septentrionalis* Fosberg. These seem to be merely ecologically induced extremes, however.

Oplismenus compositus (L.) Beauv., Ess. Agrost. 54, 1812.

NAMONUITO: Ulul Islet, observed.

NOMWIN: Nomwin Islet, observed. A common ground cover in forests.

Paspalum conjugatum Berg., Act. Helvet. Phys. Math. 7:129, pl. 8, 1762.

NAMONUITO: Ulul Islet, observed in clearings.

Thuarea involuta (Forst.f.) R. and S., Syst. 2: 872, 1817.

NAMONUITO: Ulul Islet, observed. Common on most islets, especially in shaded or partly shaded strand locations.

Saccharum officinarum L., Sp. Pl. 54, 1753.

MURILO: Ruo Islet, observed, cultivated in village. Sugar cane.

CYPERACEAE

Cyperus ferax L.C. Rich., Act. Soc. Hist. Nat. Paris, 1: 106, 1792.

NAMONUITO: Pisarach Islet, in taro swamp, July 2, 1957, Stone 2138.

Eleocharis geniculata (L.) R. and S., System. Veg. 2: 150, 1817.

NAMONUITO: Pisarach Islet, in taro swamp, July 2, 1957, Stone 2139.

Finbristylis atollensis St. John, Pacific Sci. 6: 145–150, fig. 2, 1952.

NAMONUITO: Pisarach Islet, along strand, July 2, 1957, Stone 2152.

MURILO: Ruo Islet, lagoon shore, July 5, 1957, Stone 2180. Observed on all islets. An abundant rosette former, common in exposed coastal situations, frequently in association with *Eragrostis amabilis*. The flowering scapes are highly variable in length, amount of branching, and number of spikes produced.

PALMAE

Cocos nucifera L., Sp. Pl. 1188, 1753.

On all islets. N.v. "nu."

ARACEAE

Alocasia macrorrhiza (L.) Schott ex Schott and Endlicher, Melet. Bot. 1: 18, 1832.

Observed on all islets. N.v. "oht."

Colocasia esculenta (L.) Schott, ex Schott and Endlicher, Melet. Bot. 1: 18, 1832.

NAMONUITO: Pisarach Islet, observed in taro swamps. Cultivated, less common than the following species. The plants on Pisarach were pink petioled, the petioles set with a few basal prickles.

Cyrtosperma chamissonis (Schott) Merrill, Philippine Jour. Sci. Bot. 9: 65, 1914.

Observed on all islets.

AMARYLLIDACEAE

Zephyranthes rosea (Spreng.) Lindl., Bot. Reg. t. 821, 1824.

NAMONUITO: Ulul Islet, cultivated in village. A small pink-flowered ornamental. N.v. "kaje."

Crinum asiaticum L., Sp. Pl. 292, 1753.

Observed on most islets. N.v. "kiup."

TACCACEAE

Tacca leontopetaloides (L.) Ktze., Rev. Gen. Pl. 704, 1891.

Observed on all islets. N.v. "mukmuk."

MUSACEAE

Musa paradisiaca L., Sp. Pl. 1043, 1753.

Observed on all islets. Both plantains and eating bananas are planted, often in or near taro patches, and around villages, on all the inhabited islets. N.v. "ul."

ZINGIBERACEAE

Hedychium coronarium Koenig ap. Retzius, Obs. Bot. 3: 73, 1783.

NAMONUITO: Pisarach Islet, in taro swamp, July 2, 1957, Stone 2145. Flowers white. N.v. "zinzer" (English corruption).

Subclass *DICOTYLEDONAE*

CASUARINACEAE

Casuarina equisetifolia L., Amoen. Acad. 4: 153, 1759.

NAMONUITO: Ulul Islet, observed. Introduced.

PIPERACEAE

Piper fragile? Bentham.

NAMONUITO: Ulul Islet, climbing and terrestrial, abundant, June 22, 1957, Stone 2079. Observed on all islets. N. v. "adogobwe." The determination is doubtful.

Piper ponapense C.DC., Engler's Bot. Jahrb. 56: 502, 1921.

NAMONUITO: Ulul Islet, climbing on breadfruit tree, June 22, 1957, Stone 2078.

NOMWIN: Nomwin Islet, observed.

MURILO: Ruo Islet, observed.

MORACEAE

Artocarpus incisus (Thunb.) L.f., Suppl. Pl. 411, 1781.

Abundant on most islets. N.v. "mai."

Ficus tinctoria Forst.f., Prodr. 76, 1786.

NAMONUITO: Magur Islet, large tree in breadfruit-*Pisonia-Eugenia* forest, seedlings frequent, June 29, 1957, Stone 2103. Observed on most islets. N.v. "mok."

Ficus sp. (aff. *ramentacea* Roxb.?)

NAMONUITO: Pisarch Islet, tree with basally auriculate leaves, sterile, July 2, 1957, Stone 2051.

URTICACEAE

Fleurya ruderalis (Forst.f.) Gaud., Freyc. Voy. Bot. 497, 1826.

NAMONUITO: Magur Islet, weed in village, June 29, 1957, Stone 2127.

Pipturus argenteus (Forst.f.) Wedd., DC. Prodr. 16: 235, 1869.

NAMONUITO: Magur Islet, in shrub woodland near lagoon shore, June 29, 1957, Stone 2125.

Pilea microphylla Liebm., Vidensk. Selsk. Skr. 5(2): 302, 1851.

NAMONUITO: Ulul Islet, terrestrial or on coral boulders or cement walls, observed.

AMARANTHACEAE

Achyranthes aspera L., Sp. Pl. 204, 1753.

NAMONUITO: Ulul Islet, weed in village, June 22, 1957, Stone 2081.

NYCTAGINACEAE

Bougainvillea spectabilis Willd., Sp. Pl. 2: 348, 1799.

MURILO: Ruo Islet, cultivated in village. Native of Madagascar.

Mirabilis jalapa L., Sp. Pl. 177, 1753.

NAMONUITO: Magur Islet, observed in village. Native of Mexico.

Pisonia grandis R. Br., Prodr. 422, 1810.

NAMONUITO: Magur Islet, in *Pisonia-Eugenia-Artocarpus* forest, June 29, 1957, Stone 2098. N.v. "mahk."

PORTULACACEAE

Portulaca oleracea L., Sp. Pl. 445, 1753.

NAMONUITO: Pisarach Islet, in sand near shore, July 2, 1957, Stone 2149.

Portulaca samoensis v.Poelln., Fedde Rep. Sp. Nov. 33: 163, 1933.

NAMONUITO: Pisarach Islet, in sand near shore, July 2, 1957, Stone 2150.

LAURACEAE

Cassytha filiformis L., Sp. Pl. 35, 1753.

Observed on all islets, in savannahs and outer strand forest, climbing parasitically on various species.

HERNANDIACEAE

Hernandia sonora L., Sp. Pl. 981, 1753.

NAMONUITO: Ulul Islet, observed. Present on most islets. N.v. "ojal."

CAPPARIDACEAE

Crataeva speciosa Volkens, Engler's Bot. Jahrb. 31: 463, 1902.

NAMONUITO: Magur Islet, in *Pisonia-Eugenia* forest, small tree with ternate leaves, June 29, 1957, Stone 2095.

MURILO: Ruo Islet, observed. A small tree with ternate leaves, white clawed petals, and pendent, long ovoid, brownish-green and white-flecked fruits which are edible when cooked. Native to Caroline Islands, occasionally cultivated. N.v. "afúch."

LEGUMINOSAE

Caesalpinia pulcherrima (L.) Sw., Obs. Bot. 166, 1791.

MURILO: Ruo Islet, cultivated in village. Native of Tropical America.

Canavalia maritima (Aublet) Thouars, Desv. Jour. Bot. 1: 80, 1813.

NAMONUITO: Magur Islet, observed. Pisarach Islet, lagoon shores, climbing on *Scaevola*, flowers pink, July 2, 1957, Stone 2147. Observed on most islets.

Derris elliptica (Roxb.) Bentham, Linn. Soc. Bot., Jour., Suppl. 4: 111, 1860.

NAMONUITO: Ulul Islet, observed in clearings and open woods. N.v. "up."

Sophora tomentosa L., Sp. Pl. 373, 1753.

MURILO: Ruo Islet, lagoon shores, July 5, 1957, Stone 2176.

Vigna marina (Burm.) Merrill, Interp. Herb. Amboinense, 285, 1917.

NOMWIN: Fananu Islet, creeping in woods, July 4, 1957, Stone 2170. N.v. "olu" (Namonuito), "ulu" (Nomwin).

RUTACEAE

Citrus aurantifolia (Christm.) Swingle, Wash. Acad. Sci., Jour. 3: 465, 1913.

NAMONUITO: Pisarach Islet, observed. The lime, cultivated on most islets.

SIMARUBACEAE

Soulamea amara Lamarck, Encycl. Meth. 1: 449, 1785.

NAMONUITO: Ulul Islet, along shore, June 22, 1957, Stone 2075. Pisarach Islet, observed.

Suriana maritima L., Sp. Pl. 284, 1753.

MURILO: Ruo Islet, along lagoon shore, July 5, 1957, Stone 2175.

EUPHORBIACEAE

Codiaeum variegatum (L.) Bl. var. *pictum* (Lodd.) Muell.-Arg., DC. Prodr. 15: 1119, 1866.

NAMONUITO: Ulul Islet, observed in village. A widely cultivated ornamental hedge plant.

Euphorbia Chamissonis (Klotzsch and Garcke)

Boissier, DC. Prodr. 15(2): 14, 1862.

NAMONUITO: Ulul Islet, on sandy open beach, in full sun, June 22, 1957, Stone 2080. Observed on several islets.

Euphorbia hirta L., Sp. Pl. 454, 1753.

NAMONUITO: Ulul Islet, observed. Present on most islets.

Euphorbia thymifolia L., Sp. Pl. 454, 1753.

NAMONUITO: Ulul Islet, observed.

Phyllanthus niruri L., Sp. Pl. 981, 1753.

NAMONUITO: Magur Islet, in village, June 29, 1957, Stone 2105. N.v. "sigamör." The above three species are common weeds.

Glochidion sp. (aff. *ramiflorum* Forst.).

NOMWIN: Nomwin Islet, abundant low shrubs in forest, seeds red, July 3, 1957, Stone 2163.

NAMONUITO: Ulul Islet, observed, rare. (Collected also on Truk, Stone 2047 and 2055). N.v. "efar." Until a monographic treatment of *Glochidion* appears, it seems best to leave this unnamed.

SAPINDACEAE

Allophylus timorensis (DC.) Blume, Rhumphia 3:130, 1847.

NAMONUITO: Magur Islet, in coastal woods, common, June 29, 1957, Stone 2102. Observed on most islets. A ternate-leaved shrub or small tree with spikes of small greenish flowers which produce small globose red berries. N.v. "ngö."

TILIACEAE

Triumfetta procumbens Forst. f., Prodr. 35, 1786.

Observed on all islets. A common prostrate creeper of sandy shores among grasses and low shrubs. Leaves usually somewhat 3-lobed, thick, rough; flowers yellow; fruits prickly. N.v. "ara."

MALVACEAE

Hibiscus rosa-sinensis L., Sp. Pl. 694, 1753.

NAMONUITO: Ulul Islet, observed, ornamental shrub in village.

Hibiscus tiliaceus L., Sp. Pl. 694, 1753.

NAMONUITO: Pisarach Islet, abundant in swamp, observed. Observed on several islets, along sandy shores.

GUTTIFERAE

Calophyllum Inophyllum L., Sp. Pl. 513, 1753.

NAMONUITO: Magur Islet, large tree on shore, June 29, 1957, Stone 2116. Observed on all islets. N.v. "ráguch."

CARICACEAE

Carica Papaya L., Sp. Pl. 1036, 1753.

Observed on all islets. N.v. "bwebwao" (Magur), "kipwae" (Ono).

BARRINGTONIACEAE

Barringtonia asiatica (L.) Kurz, Asiatic Soc. Bengal, Jour. 45: 70, 1876.

NAMONUITO: Magur Islet, in coastal woods, June 29, 1957, Stone 2117. Observed on most islets. The fruits are used to poison fish. N.v. "kul."

RHIZOPHORACEAE

Bruguiera conjugata (L.) Merrill, Philippine Jour. Sci., Bot. 9: 118, 1914.

This is forma *alba* n. f. In calyci albi differet. Like the species but with white rather than red calyces.

NAMONUITO: Pisarach Islet, in swamp, July 2, 1957, Stone 2144 (type). N.v. "ong."

COMBRETACEAE

Terminalia samoensis Rech., Fedde, Rpt. Sp. Nov. 4: 229, 1907.

NAMONUITO: Magur Islet, shrub in coastal woods, flowers white, drupes red, June 29, 1957, Stone 2113. Observed on most islets. N.v. "kön."

MYRTACEAE

Eugenia javanica Lam., Encycl. Meth. 3: 200, 1789.

NAMONUITO: Magur Islet, in *Pisonia-Eugenia-Artocarpus* forest, June 29, 1957, Stone 2097. Observed on most islets. N.v. "fániep."

ONAGRACEAE

Jussiaea suffruticosa L., Sp. Pl. 388, 1753.
NAMONUITO: Pisarach Islet, in taro swamp, July 2, 1957, Stone 2140.
NOMWIN: Nomwin Islet, observed.

ARALIACEAE

Nothopanax scutellarium (Burm. f.) Merrill, Interp. Herb. Amboinense 409, 1917.
NAMONUITO: Ulul Islet, observed. A common hedge plant in villages.

APOCYNACEAE

Nerium oleander L., Sp. Pl. 229, 1753.
NAMONUITO: Ulul Islet, observed in village.
Ochrosia oppositifolia (Lamarck) K. Schum., Nat. Pflanzenfam. 4(2): 156, 1895.
NAMONUITO: Magur Islet, in coastal forest, abundant, June 29, 1957, Stone 2108. Observed on most islets. A common littoral tree, often tending to form pure stands, with long-obovate glossy leaves, small white linear-petalled flowers, twinned fruits, and abundant milky sap. N.v. "umwá."
Plumeria rubra L., Sp. Pl. 209, 1753.
NAMONUITO: Pisarach Islet, cultivated in village, flowers yellow and white, July 2, 1957, Stone 2146. Observed on Ruo Islet. Native of tropical America. N.v. "séur." (On Truk this word, pronounced "sour," is applied to a species of *Fagraea;* on Ponape, pronounced "sair," to *Fagraea sair* Gilg and Benedict.)

ASCLEPIADACEAE

Asclepias curassavica L., Sp. Pl. 209, 1753.
NAMONUITO: Pisarach Islet, cultivated in village, observed. Magur Islet, in clearing, observed.

CONVOLVULACEAE

Ipomoea Batatas (L.) Poir. ex Lamarck, Encycl. Meth., 6: 14, 1804.
MURILO: Ruo Islet, cultivated. The sweet potato.
Ipomoea gracilis R. Br., Prodr. 484, 1810.
NAMONUITO: Magur Islet, in clearing, June 29, 1957, Stone 2120. Observed on most islets.
Ipomoea pes-caprae (L.) Sweet, Hort. Sub. Lond. 35, 1818.
NAMONUITO: Ulul Islet, observed on sandy beaches. Common on most islets.

BORAGINACEAE

Cordia subcordata Lamarck, Tabl. Encycl. 1: 421, 1791.
NAMONUITO: Magur Islet, in coastal forest, flowers orange, June 29, 1957, Stone 2109. N.v. "anögut."
Messerschmidia argentea (L.)I.M. Johnston Arnold Arboretum Jour. 16: 164, 1935.
NAMONUITO: Magur Islet, in coastal forest, June 29, 1957, Stone 2112. Observed on all islets. N.v. "jin."

VERBENACEAE

Clerodendrum inerme (L.) Gaertner, Fruct. et Seminif. Pl. 1: 271, 1788.
NAMONUITO: Pisarach Islet, scandent shrub in swamp area, July 2, 1957, Stone 2141. N.v. "ula."
Callicarpa cana L., Mant. 2: 198, 1771.
NAMONUITO: Ulul Islet, in forest, June 22, 1957, Stone 2082.
MURILO: Ruo Islet, in forest, July 5, 1957, Stone 2177. A fish poison.
Premna obtusifolia R.Br., Prodr. Fl. N. Holl., 512, 1810.
NAMONUITO: Ulul Islet, in clearing, June 22, 1957, Stone 2077. Pisarach Islet, in swamp, July 2, 1957, Stone 2143. Observed on most islets. For a discussion of the nomenclature of this variable species, see Fosberg, 1953.

SOLANACEAE

Nicotiana tabacum L., Sp. Pl. 180, 1753.
NAMONUITO: Ulul Islet, observed. Magur Islet, June 29, 1957, Stone 2124. N.v. "tabák."

RUBIACEAE

Guettarda speciosa L., Sp. Pl. 991, 1753.
NAMONUITO: Magur Islet, in coastal forest

along beach, flowers white, June 29, 1957, Stone 2110. Observed commonly on most islets. N.v. "mosér."

Hedyotis biflora (L.) Lamarck, Tabl. Encycl. 1: 272, 1791.

NAMONUITO: Magur Islet, weed, June 29, 1957, Stone 2122.

Morinda citrifolia L., Sp. Pl. 176, 1753.

NAMONUITO: Magur Islet, in coastal forest, June 29, 1957, Stone 2099. Observed on all islets. N.v. "nen."

CUCURBITACEAE

Cucurbita Pepo L., Sp. Pl. 1010, 1753.

MURILO: Ruo Islet, observed in cultivation.

NAMONUITO: Magur Islet, cultivated, June 29, 1957, Stone 2126. N.v. "panke."

GOODENIACEAE

Scaevola frutescens (Miller) Krause, Pflanzenreich 54 (IV, 277): 125, 1912.

NAMONUITO: Magur Islet, along strand, June 29, 1957, Stone 2111. Observed commonly on all islets. N.v. "nöt" or "nŭt."

COMPOSITAE

Synedrella nodiflora (L.) Gaertner, Fruct. et Seminif. Pl. 2: 456, pl. 171, fig. 7, 1791.

NAMONUITO: Ulul Islet, observed. A common tropical weed.

Vernonia cinerea (L.) Less., Linnaea 4: 291, 1829.

NAMONUITO: Ulul Islet, observed. A weed present on most islets.

Wedelia biflora (L.) DC. ex Wight, Contr. Bot. Ind. 18, 1834.

NAMONUITO: Magur Islet, in forest, June 29, 1957, Stone 2092. Observed on all islets, common. N.v. "atugat" (Magur), "adiat" (Ono).

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